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by

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Declaration

The material contained in this thesis has not previously been submitted for a degree at the University of Durham or any other university. The research reported within this thesis has been conducted by the author unless otherwise indicated.

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Abstract

The conservation and management of tropical deer populations need both knowledge of the ecology and natural history of deer and an understanding of the utilization of deer populations by humans. The south-eastern portion of the Yucatan Peninsula in Mexico is the region with the largest ungulate diversity in Mesoamerica, including three of the five species of deer found in Mexico. For centuries, human populations have been harvesting deer for subsistence in this region. Little is know on the ecology and conservation of ungulate populations undergoing subsistence harvesting in Mesamerica.

This thesis is the result of a long-term study (1996-2001) on the population, community ecology and sustainable management of the Yucatan Peninsula brown brocket deer (*Mazama pandora*), red brocket deer (*Mazama americana*) and white tailed deer (*Odocoileus virginianus*) in the Greater Calakmul Region (GCR), south-eastern Mexico. Chapter two addresses the estimation of deer abundance, densities, population structure and habitat use of sympatric populations of these three species of deer. Chapter three outlines the relationships of the deer diet with aspects of habitat ecology such as fruit phenology, availability and seasonality. Chapter four describes the spatial and temporal patterns of subsistence hunting of tropical deer populations with the use of a novel technique incorporating both GIS/GPS technologies and participatory research.

The abundance of deer in the GCR remained stable during a continuous monitoring period of five years and no effects of hunting were detected in the populations of the two *Mazama* species. A steady decline was detected in the populations of white-tailed deer that might be attributed to over-harvesting by subsistence hunters. Densities of the three species of deer are similar or higher that those reported elsewhere in the Neotropics. *Mazama americana* presented strong preferences in habitat use for the Tall Perennial Forest, while *M. pandora* and *O. virginianus* used habitats in relation with availability. The population structure of the three species of deer resembles a stable population with the majority of individuals found in younger age classes but older individuals still found in ages above 12 years old (the cementum annuli technique for age determination was used for the first time in a tropical deer population). *Mazama americana* is a frugivore deer with its diet composed of up to 80% fruits year-round, while *M. pandora* and *O.virginianus* are both frugivores and browsers. Fruit availability for deer was strongly linked with fruit phenological patterns of the major plant species composing the deer diet year-round. A critical period with low fruit availability and potential dietary stress for deer was found during the dry season (April-May). The Zapote tree (*Manilkara zapota*) might be a keystone plant resource in the region.

Subsistence hunting of deer is widespread in the GCR region, but deer hunting seems to be sustainable in part due to the dynamic patterns in spatial and temporal location of hunters in the landscape. The spatial and temporal patterns of deer hunting might be responsible for the creation of natural refuges and source/sink areas for deer populations. The conservation and management of tropical deer populations in the GCR and Meso-America are discussed in the light of these findings.

To the memory of my father

Enrique Weber

(1927-2001)

Acknowledgements

Many things have changed since that cold morning of November 1995 at the top of the Structure III (the highest Mayan pyramid) in the Calakmul Archaeological site, when the magical combination of the sight of "a sea of trees" (extending as far as the horizon line to 360 degrees), the sounds of the jungle (including those amazing echoes coming from countless parrots and toucans, howler monkeys and crested guans) and the sheer beauty of a day-break in one of the true last frontiers of civilization on earth, hook me forever to the thrills and frustrations of tropical ecological research in the southern Yucatan peninsula, Mexico. This long-term project (1996-2004) would have never been possible without the help of a number of people that participated in its conception, long gestation period and even longer delivery phase.

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CHAPTER ONE

1.1 Introduction

1.1.1. The search for sustainability in wildlife utilization.

The astonishing diversity of ecosystems in Latin America is one the main characteristics that early colonizers and naturalists detected when they arrived to the new world. Later, as they travel through the region, cultural human diversity was also recognized as a main feature of this biologically and culturally reach lands.

Early naturalists, such as Fray Bernardino de Sahagun, an interpreter monk with the Spanish Franciscan missions in what it is now Mexico, became interested in natural history and philosophy and depicted a premature curiosity in the description of all new animal and plant species in the post-colonial Mesoamerica of 15th century (Leopold, 1977). It was this interest by the early colonial naturalists that allow us to appreciate today the deep knowledge that indigenous people has had (and still have) in the biological resources they are dependent. For centuries, these people had relied in this knowledge of natural history to take advantage when harvesting natural resources such as fruit crops and game hunting.

While most cultural anthropologists and ecologists today recognize the wealth of natural history knowledge in native American nations, they also acknowledge that despite this relative understanding of biological patterns and processes there is still much to be learn on the relationships between native American people and their natural resources (Terborgh and Van Schaik, 2002) . In particular, the early anthropological concept of the "ecologically noble savage" (Alvard, 1993), that postulates that indigenous people intrinsically manage their natural resources in a sustainable manner is been heavily challenged with the overwhelming evidence to the contrary gathered in the last 20 years of both ecological and anthropological research in Latin America (Robinson and Bennett, 2000; Terborgh and Peres, 2002).

Some argue that conservation through sustainable use has no evolutionary precedent (Van Schaik and Rijksen, 2002; Terborgh *et al.,* 2002). Our closest living relatives, the great apes, are extremely wasteful feeders, drooping fruits that are not yet ripe instead of leaving them on the tree to ripen (Van Schaik and Rijksen, 2002). Our own species does

not act very differently from these behavioural patterns. Several detailed field studies on both prehistoric and modern hunters have demonstrated a lack of any conservation ethic (Alvard, 1998; Robinson and Bennett, 2002). In prehistoric times, prey was harvested until local extinctions occurred or it was hard to find and man and its tribes simply move to new hunting territories to start the same process all over again. Several prehistoric extinctions of mega-fauna, such as the Mastodon or the Giant sloth are strongly linked to over-harvesting by human hunters (Stiner *et al.,* 1999). Archaeological evidence shows similar events during the Pleistocene. In the Mediterranean for example, hunters first depleted marine turtles and shellfish and then had to turn to small mammals and birds (Stiner *et al.,* 1999). Thus, like our great-ape cousins, humans do not posses any inherent predisposition to conserve or manage natural resources for the future and so guarantee sustainable use. The "noble savage" probably does not exist except perhaps in the mind of a few romantic anthropologists and writers (Van Schaik and Rijksen, 2002).

Today, unsustainable use is one of the most complex problems that the science of tropical conservation is facing. Commercial and subsistence hunting has left many regions and even protected areas such as accessible parks empty of wildlife large enough to be worth the price of a shotgun shell (Redford, 1992; Robinson and Bennett 2000). The "empty forest" as this syndrome of apparently "healthy" forests ecosystems but without their main faunal components is sometimes referred to, has become a symbol of unsustainability of resource use in modern times and a definition of what humans can accomplish in the long term if the harvesting of finite natural resources is not controlled or managed to some degree.

In many regions of the world and in Latin America in particular, the combination of extreme poverty, rapid population turn-over, frontier areas of colonization and availability of large forested areas, come together as the perfect "recipe for disaster" when looking for the protection of endangered species from unsustainable use (Fitzgibbon *et al.,* 2000).

1.1.2. Subsistence hunting

As the tropical wilderness is opened to the advance of western civilization by road building and subsequent colonization, the original inhabitants are increasingly

being pushed into smaller portions of the original territories and traditional harvesting practices have been abandoned (Alvard, 1998; Towsend, 2000). Indigenous people are concerned about loosing their territorial ancestral lands because they are dependant on the harvest of natural resources to make their livelihood (Peres, 2001).

Biodiversity, the diversity of life on earth, currently is declining at rates rarely seen previously in the history of the world—with extinction by some estimates reaching 1,000 species annually (Robinson and Bennett, 2000). At the same time, the number of people on earth has grown to unprecedented levels, with global population reaching 6.3 billion in late 2003 (U.S. Bureau of the Census 2003). The precipitous decline of biodiversity in a period of enormous human numbers led many to equate a large human population with biodiversity decline (Ehrlich, 1995) with the loss of vast areas of natural habitat and the rapid extraction of resources, helping to explain the widespread loss of plants and animals.

One of the more recent conservation concerns has been the effect of subsistence hunting on tropical wildlife populations in frontier regions of colonization (but see Robinson and Bennett, 2000 and references therein). While humans living in these remote regions may harvest an incredible amount and diversity of wildlife for subsistence reasons (Towsend, 1995), the majority of the hunting biomass in tropical forests is provided by ungulates with antelopes, deer, wild pigs and peccaries leading the list as the main providers of animal protein around the tropical world (Hurtado-Gonzalez and Bodmer, 2003; Escamilla *et al.*, 2000; Peres, 2000; Weber, 2000).

1.1.3.Hunting and tropical deer populations

Despite the fact that deer has been recognized as a major game species for hunters in several studies in the tropical realm (Hurtado-Gonzalez and Bodmer, 2003; Weber, 2000) the management of deer populations in Latin America is hampered by the lack of knowledge on the natural history and ecology of most of the 18 species of deer currently inhabiting the continent (Appendix I). Some genus and several species of deer have been completely ignored by local and international scientists and for some of them even the most basic information on geographic distribution and abundance is completely absent (Weber and Gonzalez, 2003; see Appendix I).

Ironically, while ungulates and deer in particular play an important role as prey species in many regions of Latin America and help sustain entire humans populations by providing high quality animal protein, the local governments has had little interest in managing this important game resource. Some of the most poorly known and least understood ungulates worldwide are deer of the genus *Mazama*. This genus comprises five recognized species and three recently discovered or proposed new species (Appendix I). Most *Mazama* deer are forest dwellers of interior tropical rain forests and are solitary inconspicuous animals that for years have been ignored by mammalogists and ecologists. Yet, deer of the genus *Mazama* might provide from 55 up to 70% of the total wildlife harvest biomass by subsistence hunters in some Neotropical forests (Hurtado-Gonzalez and Bodmer 2004). The importance of disentangling the ecology of deer of the genus *Mazama* is therefore imperative if we are to understand the intricate relationships between human hunters and one of their most important prey bases in the Neotropical realm.

In order to develop ecologically sound conservation and management plans for deer populations undergoing harvesting by subsistence hunters it is imperative to obtain baseline information on the natural history and ecology of deer and both the socio-economical and ecological aspects of the human harvest scenario.

This thesis is an attempt to this regard with two of the least know deer species in Latin America: The Yucatan Brown brocket deer (*Mazama pandora*), recently re-discovered by modern science (Medellin *et al.*, 1998), the red brocket deer (*Mazama americana*) one of the most widespread but poorly understood forest dweeling ungulates and the most common and widespread white-tailed (*Odocoileus virginianus)*. The study took place in one of the last frontiers of civilization and development in Mesoamerica, where hunting for a living still remains as a major subsistence activity: The tropical forests of the Mayan jungle in the central Yucatan Peninsula, southeastern Mexico.

1.2. Study area

1.2.1. The Greater Calakmul Region, south-eastern Mexico.

With humans living throughout most of the terrestrial world, conservationists have sought varying solutions to protect remaining biodiversity. One possible solution proposed by the United Nations Educational, Scientific, and Cultural Organization (UNESCO) was the concept of Biosphere Reserve, a protected area that incorporates biodiversity conservation, economic development, and research and monitoring associated with the first two functions (UNESCO 2002). The network of Biosphere Reserves include hundreds of protected areas in the countries that harbors most of the biological diversity, including Mexico. In the southeastern portion of the Yucatan Peninsula "Calakmul" was designated as a protected area by the Mexican government in 1989 and was named a biosphere reserve in 1993 (Stedman-Edwards 1999).

Decreed by presidential mandate in 1989 with the highest protection status available in Mexico, the 1,786,267 acre (723,185 ha) Calakmul Biosphere Reserve is the largest protected area of tropical forest in Mexico and one of the largest in the whole of Mesoamerica. The site is situated in the new Ecological Municipality of Calakmul in the southern state of Campeche. Calakmul is part of the Mesoamerican Corridor which stretches from northern Quintana Roo to the tropical forests of Peten in Guatemala and Montes Azules in Chiapas. It protects numerous archeological sites from the great Maya culture, which reached its peak in the late classic period. Archaeological centres such as Balamku, Hormiguero, Chicanna, Río Bec and Calakmul stand as testimonies of the area's rich cultural heritage. In 1993 Calakmul was designated a UNESCO Man and the Biosphere site. Today, most people refer to the Calakmul region (including the Calakmul municipality, biosphere reserve, buffer and corridor areas around it) as the Greater Calakmul Region (GCR) and this name will therefore be used in this document when making reference to this eco-geographical region.

In this work, the GCR is defined as the geographical area comprised between the 90°, 20' and 89°, 00' west; and 19°, 15 and 17°, 50' north. Most of the work on deer ecology and subsistence hunting was carried out in what is known as the Zoh-Laguna plateau, located among the parallels 89° 45' and 89°, 15' west. This area in particular contain the highest elevation points in the GCR with altitudes of 250 to 350 meters above sea level.

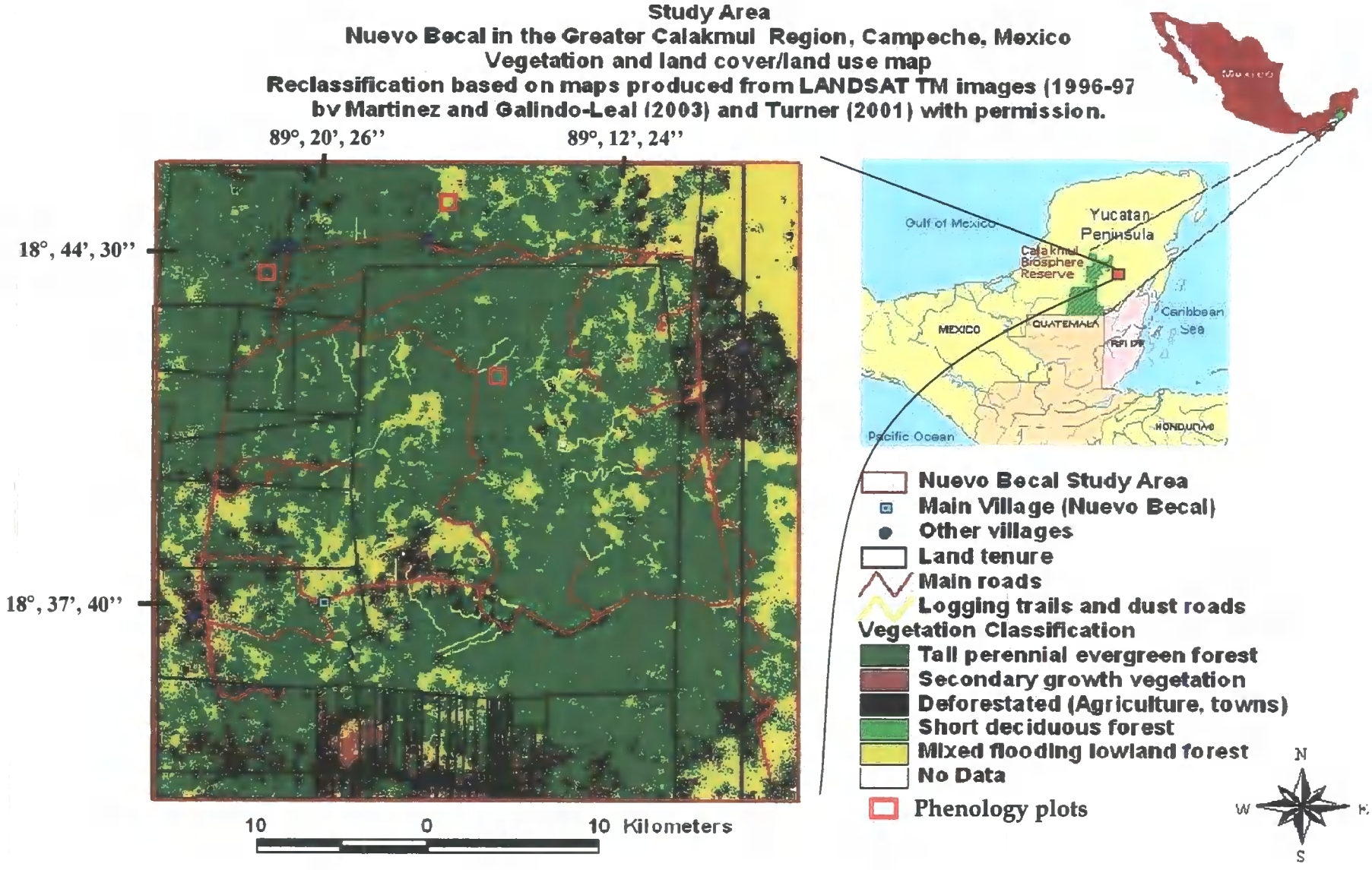

Figure 1.1. Map of the study area, Nuevo Becal Community in the Grater Calakmul Region, Campeche, Mexico.

The community of Nuevo Becal and other human settlements studied in this project are located in the centre of the Zoh-Laguna plateau (figure 1).

The GCR and the reserve it include are important elements in a larger system of protected areas which form an ecological corridor of over two million hectares stretching between central Yucatan and the Belizean forests (see Figure 1). The main objective of the Calakmul Biosphere Reserve is the long-term maintenance of biodiversity. Accepted into the UNESCO network of biosphere reserves in 1993, the Calakmul Biosphere Reserve is divided into core and buffer zones. Although to date no management plan has been implemented, the general understanding is that ecologically-sustainable production activities are allowed within the buffer zone while no human activity is permitted within the core zone (Galindo-Leal *et al.*, 2000). Conflict arises from the fact that the borders of the core zone cut across the territory of pre-existing ejido communities (an ejido is a land grant administered by a group of individuals called ejidatarios who hold the usufruct rights to their land or ejido) accorded to them by the Mexican federal government and privately held properties. Agriculture, forestry, cattle-ranching and subsistence-level hunting are practiced on ejido and privately held lands that overlap with the reserve.

Calakmul Biosphere Reserve encompasses slightly more than 723,000 ha but the whole of the GCR probably reaches around 1 million ha when all the forested private and communal (ejido) lands are considered. Comprising the largest protected tract of tropical forest remaining in Mexico, Calakmul is one component of the Maya Forest, a large expanse of tropical forest extending over several states in Mexico, western Belize, and northern Guatemala that in total sums up for more than 2.5 million hectares; that is the largest continuous tropical forest north of the Amazon (Figure 1).

1.2.1.1. Ecological Significance

With its large tracts of tropical forests, the GCR possesses great natural and cultural assets. A mix of old growth, medium semi-evergreen and seasonally inundated lowland forests, as well as grasslands, makes the site a refuge for a great variety of animal species, including threatened species such as jaguar (*Panthera onca*), puma (*Puma concolor*), tapir (*Tapirus bairdii*), black howler monkey (*Alouatta pigra*), Central American spider monkey (*Ateles geoffroyi*), anteater (*Tamandua mexicana*), ocellated

turkey (*Agriocharis ocellata*), great curassow (*Crax rubra*), keel-billed toucan (*Ramphastos sulfuratus*), king vulture (*Sarcoramphus papa*), and many more. This tropical forest, together with the rest of the Mesoamerican Corridor, allows for the movement of species from the Yucatan province (sub-xeric) to the Peten isthmus (subhumid and humid) and is also an important wintering ground for several migratory bird species. Thirty percent of the bird species sighted in the reserve breed in the United States and Canada and use these forests as their wintering grounds (Berlanga and Wood, 1997). Some of these neotropical migrants such as the hooded warbler *(Wilsonia citrina*) and the Swainson's warbler (*Limnothlypis swainsonii*), are threatened or endangered species (SEMARNAP, 2000). The site is unique with regards to the number of rare, endemic, species in danger of extinction and special protection species in Mexico; including six of seven species of marsupials, two of three primates, two of four edentates, and five of six species of felines; jabiru stork, king vulture, elegant eagle, three species of toucans, several species of parrots, Moreletti crocodile, *Ctenosaura* iguana, Claudius tortoise and the endemic and extremely rare *Triprion petasatus* tree frog. Flora of the site includes the only *Canellasea* family on the American continent, six endemic genre, five threatened species, two rare species, and 380 endemic species among the more than 420 species of trees described so far the GCR represents the last stronghold for the conservation of pure stands of Guayacan (*Guayacum sanctum*) forests in the world (Martinez and Galindo-Leal, 2003).

1.2.1.2. Socio-economic context

At the beginning of the colonial period approximately 20,000 Mayans lived in GCR dense forests, practicing traditional agriculture and hunting activities. In the early 20th century the extraction of chicle (the natural resin obtained from zapote trees to produce chewing gum) and wood became important in the region, new roads were built and many small scattered human settlements established in the area. At present approximately 23,700 people from 23 different states live in 72 settlements, most of them located on the eastern side of the reserve. The main economic activities in the area are timber extraction, commercial and self-sustenance agriculture, ranching, honey production, subsistence hunting, tourism and small-scale commerce.

The buffer zone of the southern division of the reserve is composed of forest extension lands belonging to ejido communities north of the reserve. The Calakmul Biosphere

Reserve is a patchwork of mature disturbed forest, secondary growth vegetation of less than 25 years and savanna-type flood plains. The present state of the forest both within the reserve and in the ejido communities that surround it is a result of timber extraction, forest clearing for agriculture and cattle ranching. The most abundant tall trees include chicozapote (*Manilkara zapota*) and ramón (*Brosimum alicastrum*) (Miranda 1958; Rzedowski 1989). Prominent commercial species are mahogany *(Swietenia macrophylla*) and Spanish cedar (*Cedrela odorata*). Biological inventories indicate that 18 endemic plant species are found in the larger Peten ecosystem

Despite its geographic isolation, the reserve and its immediate surroundings experienced considerable population growth during the 1980s and 1990s, placing increasing pressure on resources in the region in general and on the biosphere reserve in particular. Results of the socioeconomic studies in the region (Ericson *et al.,* 1998; Steadman-Edwards, 2000) indicate that rapid population growth continued in the region through the 1990s, affecting most localities in or near Calakmul, in large part due to continued migration (likely) from other parts of Mexico. Census data reveal the presence of economic activities in or near Calakmul incompatible with conservation, and satellite imagery indicates agriculture in several parts of the biosphere, including the nuclear zone. Statistical analysis of the former indicates a significant relationship between population and agriculture, while an evaluation of agricultural suitability in and around Calakmul indicates mixed though often limited potential. As a result, continued population growth in this area will expand the agricultural footprint, likely straining Calakmul management to maintain the conservation function of the biosphere reserve (Ericson *et al.*,1998).

The reserve consists of a tropical humid forest ecosystem that includes evergreen tropical humid forest, semi-deciduous forest with temporally flooded forest, thorn forest, and tropical deciduous forest (UNESCO 2003). This ecosystem contains considerable biodiversity, including about 250 tree species, 500 butterfly species, 30 amphibian species, 100 reptile species, 280 bird species, and 100 mammal species (Galindo-Leal *et al.*, 2000). Calakmul also is home to a rich collection of (predominantly) Classic Maya archaeological sites, not only increasing the importance of conserving this part of southern Mexico but also providing evidence of substantial

prehistoric human occupation in an area that in the late 20th century would experience considerable settlement once again.

Following an historic period of relative seclusion and obscurity, in the 1970s human population began to grow in and around what would become the Calakmul Biosphere Reserve. In large part this is due to programs promoted by the Mexican government to foster development in this region, resulting in population growth in the vicinity of Calakmul. This surge in human population began attracting attention from conservationists who were concerned that the increase in human presence would negatively affect biodiversity in the reserve (Ericson 1996; Ericson *et al.*, 1999; Stedman-Edwards 1999). Examinations of data from the 1990 census of population and housing and the 1995 nation-wide population count showed that population growth had continued at a rapid rate for selected communities in and near the reserve (Ericson *et al.*, 1999). However, those studies did not explore connections between demographic change and impacts on Calakmul. There remains a need to assess how population growth possibly led to expanding agricultural activities, resource extraction, and other shifts in land use that have important implications for the conservation integrity of this key protected area (Schulze and Whitacre, 1999).

The biosphere reserve concept is an attempt to conserve biodiversity in areas that also contain people. Central to the biosphere concept is the division of each reserve into a series of three types of zones: core areas secured for biodiversity protection in minimally disturbed ecosystems; buffer zones, generally surrounding the core and allowing human activities compatible with biodiversity conservation; and transition zones, containing human settlements, agricultural fields, and other activities in which residents, government agencies, researchers, and others attempt to develop resources sustainably (UNESCO 2002).

Although historically a remote, sparsely populated area until the 1970s, the region of southern Mexico encompassing the GCR contained large numbers of people more than 1,000 years ago. With evidence of habitation and public building construction as early as 300 BC, the prehistoric Maya capital of Calakmul came to occupy 70 km 2 and contain 50,000 people at its apex during a period of occupation called Late Classic (AD 500-775) (Ericson *et al.*, 1999). The population of Calakmul survived through intensive

agriculture (primarily maize). Classic period residents deal with the key limiting factor of water through an elaborate hydraulic system based on water catchments and canals. A combination of factors, including political, economic, and environmental (a prolonged drought), likely contributed to the demise of Calakmul's Maya civilization during the ninth century AD. Human habitation in the region would not even begin to approach prehistoric levels until the late 20th century.

Available data from the 1980, 1990, and 2000 censuses of population and housing reveal a pattern of considerable population growth over the past two decades in and near Calakmul Biosphere Reserve (Instituto Nacional de Estadística, Geografía, e Informática [INEGI] 1998). These trends emerge both in the changing number of separate communities at various distances from the reserve, and in changing population (Table 1.1). In 1980, the census of population and housing recorded only 14 communities within 20 km of the reserve. By 1990, the total number of communities within 20 km of the reserve had increased to 58, and by 2000 to 203—the totals varying with placement within the reserve or within one of two 10-km bands around the reserve.

Table 1.1. Human population in the Greater Calakmul Region (1980-2000).

	Number of Communities			**Avg. Annual Change (%)**	
Geographic Area	**1980**	**1990**	**2000**	**1980-90**	**1990-2000**
Within the Reserve	2	15	42	22.3	10.8
< 10 km of Reserve	7	30	85	15.7	11.0
10-20 km of Reserve	5	13	76	10.0	19.3
	Total Population			**Avg. Annual Change (%)**	
Geographic Area	**1980**	**1990**	**2000**	**1980-90**	**1990-2000**
Within the Reserve	82	1,158	3,015	30.3	10.0
< 10 km of Reserve	2,104	6,413	11,419	11.8	5.9
10-20 km of Reserve	1,139	3,149	12,244	10.7	14.5
	Persons per Community			**Avg. Annual Change (%)**	
Geographic Area	**1980**	**1990**	**2000**	**1980-90**	**1990-2000**
Within the Reserve	41.0	77.2	71.8	NA	NA
< 10 km of Reserve	300.6	213.8	134.3	NA	NA
10-20 km of Reserve	227.8	242.2	161.1	NA	NA

Data sources: INEGI 1982, 1991, 2002.

Population statistics for these same years and geographic areas support the

trends observed among communities. In 1980, slightly more than 3,300 persons lived within 20 km of Calakmul, the total increasing to more than 10,700 in 1990 and nearly 26,700 in 2000 (Table 1.1). As with the number of communities, the growth in population between years was remarkably rapid for the three geographic regions in and around Calakmul, in one case averaging more than 30 percent annually. Much of the population added in 1990 and (especially) 2000 resided in small settlements, as indicated by the decline in the number of persons per community for some of the groups of communities near the reserve.

1.2.1.3. Geomorphology

The Calakmul region is the highest physical part of the Yucatan Peninsula. More than 380 m above the sea level, Calakmul can be considered a plateau settled on calcareous rocks (called Karst), where the rainwater dissolves the calcium carbonate and the water filters underground, forming subterranean rivers. The soils of Calakmul are mainly lithosols and rendzins with an average depth of 10 and 30 cm, respectively. Differences in the drainage capability of the rendzins are responsible for the formation of deep soils (60 cm) which can retain water seasonally, leading to the formation of Lowland flooding forests. These soils are regionally called Ak'alche in the Mayan language (Martinez and Galindo-Leal, 2003).

1.2.1.4. Hydrology

The Calakmul region, as well as almost all of the Yucatan Peninsula, does not have any large rivers. The majority of the water runs underground and only collects superficially in soil depressions (cenotes) or is naturally stored in small lagoons and water holes, regionally called "aguadas". These aguadas play an important role in the landscape because they are the only water source during the dry season for many animal species. In the Calakmul Biosphere Reserve more than 3,000 aguadas have been identified (Garcia-Gil, G. ECOSUR. personal communication. 2001)

1.2.1.5 Climate

According to Köppen (modified by Garcia 1988) the Calakmul climate is classified as warm and sub-humid (Aw), with a mean annual temperature of 24.6° C. There is

seasonal summer rainfall, with an annual average of 1076.2 mm (Figure 1.2). A clearly demarked humidity gradient decreases from south to north and east to west (Martinez and Galindo-Leal, 2003)

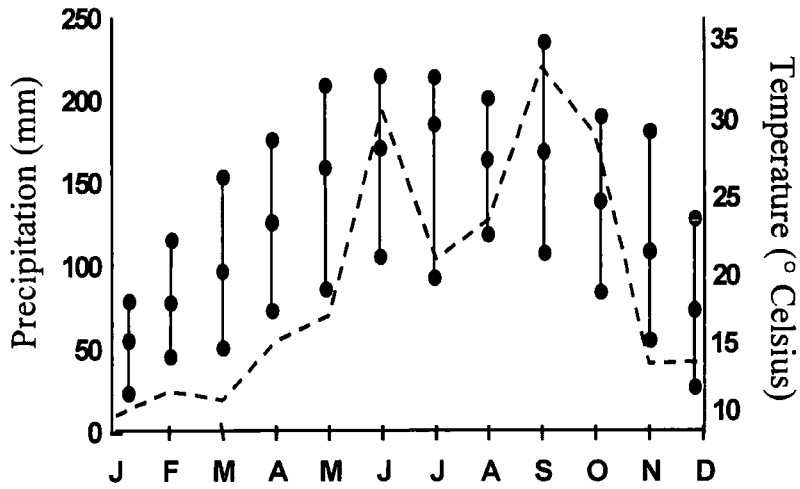

Figure. 1.2. Climate chart for the Greater Calakmul Region, Campeche, Mexico. The precipitation (dashed line) represents the average monthly rainfall pattern and the temperature (whiskers) are the media plus minimum and maximum temperatures (data from the Zoh-Laguna village meteorological station 1995-1999 obtained with permission from SAGARPA, Mexico)

1.2.1.6. Flora

The region is a mosaic of different kinds of tropical forest, ranging from low-deciduous forest in the north to tall-evergreen forest in the southeastern extreme (Miranda 1958; Rzedowski 1978). More than 1,600 plant species have been found in Calakmul, and this region contains more than 80 % of the entire number of species in the Yucatan Peninsula with 1,936 (SEMARNAP 2000). Of the different forest associations, four of the most important are (Martinez and Galindo-Leal, 2003):

Tall semi-perennial ("evergreen") forest

This forest type covers more than 50 % of the area. This is a forest where 25–50 % of the species are deciduous (loose their leaves seasonally). Tree height ranges between 15 and 25 m, and the dominants species are: *Swietenia macrophylla, Brosimum alicastrum, Lysiloma latisiliqua, Bursera simarouba, Cedrela odorata* and *Manilkara zapota* (Martinez and Galindo-Leal, 2003)

Mixed lowland flooding forest

This forest type covers around 25 to 35 % of the Calakmul area. It occurs on low-drainage soils called Ak'alche in the Mayan language. These forests are seasonally inundated and tree heights are 10 to 15 m. Characteristic species are *Haematoxilum campechianum*, *Bucida buceras*, *Metopium brownie*, *Manilkara zapota* and *Byrsonima bucidaefolia* (Martinez and Galindo-Leal, 2003)

Low semi-deciduous forest

A third common forest type present in the region is the low semi-deciduous forest, where trees average 15 m tall. Usually these forests are present in the slope of the hills or on the tops where there are many stones and dry soils. Among the species present there are *Bursera simarouba, Brosimum alicastrum*, *Guayacum sanctum*, *Lysiloma latisiliquia*, *Cedrela odorata*, *Vitex gaumery* and *Lonchocarpus xuul* (Pennington and Sarukhan 1998; Martinez and Galindo-Leal, 2003).

Second growth vegetation

A mosaic of succesional stages varying in ages from 1 to 25 years old is considered by most botanists as secondary vegetation resulting from slash and burn agricultural practices. This patches are more commonly found within the private and communal lands in the buffer areas of the Calakmul Biosphere Reserve where local ejidatarios still practice slash and burn agriculture as the main subsistence activity. After a few years of crops of corn, beans, squash and chili the fields (in average one to two hectares in size) are abandoned and the vegetation succesional process begin. Patches of 1 to 5 years old are dominated by early aggressive colonizer plants such as ferns, *Ficus sp.* and *Bursera* sp. trees. Older succesional stages (15 years and more) closely resemble the structure and composition of low semi-deciduous forests and sometimes are difficult to distinguish from this vegetation class (Martinez and Galindo-Leal, 2003)

1.2.1.7. General Fauna

Calakmul is a region with a high diversity of reptiles, birds and mammals. Fish are not well known, and only 18 species have been identified in the area. Sixteen species of amphibians and 50 species of reptiles have been reported for the Calakmul Reserve (Galindo-Leal *et al.*, 2000), and 286 species of birds have been observed in the area.

Calakmul has 94 species of mammals. Although is not as diverse as other tropical forest in Mexico, Calakmul represents one of the last remaining natural areas for the conservation of several species who need large amounts of habitat such as the tapir (*Tapirus bairdii*), white-lipped peccary (*Tayassu peccary*), jaguar (*Panthera onca*) and king vulture (*Sarcoramphus papa*), among others.

Regarding the ungulate population, Calakmul is one of the most diverse forests in ungulate species from southern Mexico. There are six species of ungulates, including the recently re-discovered Yucatan brown brocket deer (*Mazama pandora*) (Medellin *et al.*, 1998), the red brocket deer (*M. americana*), the white-tailed deer (*Odocoileus virginanus*), two species of peccaries; the collared peccary (*Peccari tajacu*) and the white-lipped peccary (*Tayassu peccari*) as well as the last element of Neotropical megafaunal, the Central American tapir (*Tapirus bairdii*).

1.2.2. Nuevo Becal community

A large part of this study was carried out in the ejido Nuevo Becal located in the eastern buffer section of the Calakmul Biosphere Reserve (18°, 44',33'' and 18°, 37', 40'' west and 89°, 20', 26'' and 89°, 12', 24'' north). This communal land-hold is one of the largest ejidos in the Calakmul municipality and is representative of the GCR. It encompasses 52,000 ha with at least 30,000 of these designated as forested area. Subsistence hunting plus timber and non-timber extraction activities are allowed in the forested area. The Nuevo Becal ejido is located 30 km from the municipality head-town (Xpujil) on the northeastern side of the GCR. Access to the community is gained through only two possible access points: one coming from the south in Xpujil and involving a 16 km drive on a relatively well maintained dust road and the other one coming from the east from Caobas ejido and involving a long 25 km drive in difficult road conditions and often impassable flooded trail and dust roads during the wet season.

The population of about 300 inhabitants includes 80 ejidatarios (family heads) and is comprised of peasants coming mainly from Veracruz, Tabasco and Campeche states. The main economic activities include agricultural (mainly maize and hot-pepper), incipient cattle raising, logging, and the extraction of non-timber products like chicle gum, xiat-palm (a palm used as ornament in Europe and U.S.), mahogany seeds and

subsistence hunting. In the last two years the ejido has been involved in a sport hunting enterprise with little success (Commissary Ejidal; Personal Communication.).
The main vegetation classes of Nuevo Becal are representative of the GCR with both Tall semi-perennial forest and Mixed lowland flooding forest dominating the forest mosaic. Major agricultural fields are located around the settlement area but some isolated slash and burn agricultural fields can be located as far as 16 kilometers from the main settlement area (Figure 1.1).

Nuevo Becal was chosen to work in this project because it has many advantages compared with adjacent or even distant more isolated communities. The large size of the land-hold guaranteed a large forest cover as opposed to smaller land-holdings where deforestation might be higher. This large forest tract in Nuevo Becal also ensured healthy wildlife populations. The community presents a network of old, abandoned logging roads in the form of a grid of trails that were cut in the 1960's when the boom for Mahogany harvest exploded. Many of this roads are impassable even with a 4 x 4 vehicle but sometimes can be used for walking. For the collection of spatial hunting data this network of trails proved to be a essential feature that does not exist in many other communities or in the Calakmul Biosphere Reserve. Moreover, Nuevo Becal is located at merely 18 km from the town of Zoh-Laguna where I bought a house and based the operations site camp fort this project

Prior to the start of this research project several informal meetings with the local community leaders (Comisariado Ejidal) and formal meetings during the traditional last-sunday-of-the-month community gathering were carried out in Nuevo Becal to let people know about the research purposes and advances as well as to reach the cooperation of local hunters willing to cooperate with the project ambitious aims in the long term. These meetings were extremely important to have a permanent presence and cooperation of the people involved and became a core component of the project through the years.

1.3. Conceptual framework

1.3.1. Thesis aims

The general aims of this thesis are three-fold:

1. To document unknown aspects on the natural history and ecology of sympatric populations of three species of tropical deer: The recently re-discovered endemic Yucatan Peninsula brown brocket deer (*Mazama pandora*), the red brocket deer (*Mazama americana*) and the white-tailed deer (*Odocoileus virginianus*) in the forest ecosystems of the Greater Calakmul Region, Campeche, Mexico.

2. To better-understand the effects of subsistence hunting on the populations of these species of deer with particular emphasis on the temporal and spatial organization of deer hunters in the forest landscape.

3. To provide ecologically sound management alternatives for deer populations subjected to intensive human hunting pressure for subsistence.

Important note:

The information presented in this and the following chapters was obtained between March 1996 to August 1999 and between March 2001 to February 2002. During this periods, I lived semi-permanently in the study area and all of the information presented here comes from systematic work from that period. I used part of the information on deer abundance (only permanent transect data) for my Master of Sciences degree (University of London, Royal Veterinary College, 2000) and a re-analysis of this data is presented in Chapter 2. However, all analyses, statistics, graphs, charts, and texts are first presented here, since another year of field work (2001) was added to the whole study. Therefore, all intellectual work (with the exception of the section on the estimation of abundance indices with permanent transect data from 1996-1999) is novel material for this PhD thesis.

1.3.2. Main research questions and hypothesis

1.3.2.1. Deer biology and ecology

During the span of the almost five years of field work (1996-2001) in the GCR, the main research questions regarding the biology and ecology of deer centred in documenting unknown baseline information on the distribution, abundance, diet and habitat use of the three species of deer.

The absolute lack of any ecological information on the *Mazama* genus north of the Amazon and a very poor understanding on the ecology of tropical white-tailed deer lead to set these very basic questions in this investigation: Where and how are these deer species distributed in the habitat mosaics that they inhabit?, How is the abundance of deer being affected by human subsistence hunting?, What is the diet of deer and how is it composed botanically?, Are the three species of deer separated in different ecological niches by differences in feeding habits or by differences in habitat use, or both?, Are the three species of deer using the habitats available to them in relation with availability or do they have habitat preferences?. While most of these questions were answered at least partially, many other specific questions and hypothesis were developed for each topic. These specific questions are better-outlined in the respective data chapters.

1.3.2.2. Subsistence hunting

A considerable number of studies on subsistence hunting have been developed in Latin American frontier regions in the past 10 years. While the majority of these studies have had an analysis of hunting sustainability as a major common factor, most if not all have uncared for the spatial and temporal patterns of hunters in the landscape. This although unfortunate is understandable, because obtaining precise spatial and temporal information on subsistence hunting is extremely difficult and time consuming. Moreover many previous studies were carried out before the advent and availability of modern geo-referencing and geo-spatial techniques such as GPS and GIS.

In this thesis, I will present the first attempt on approaching the subsistence hunting problem in tropical forests from a spatial and temporal perspective with the help of both GPS/GIS technology and participatory research.

The main questions regarding deer hunting from a spatial and temporal perspective were: What is the spatial and temporal allocation of hunters in the landscape?, How are hunting catchments formed and organized in time and space? Is the spatial and temporal location of hunters supporting the hypothesis of hunters being central place foragers?, What is the influence of roads in deer hunting human behaviour and patterning?. And finally; Is the spatial and temporal location of hunters affecting deer populations? If so, is this effect positive or negative from a conservation perspective?

All of these questions were partially or totally addressed in Chapter 4 and some of the potential consequences of the answers are discussed in both Chapter 4 and 5.

1.3.3. Thesis outline and organization

This thesis is organized into five chapters and three appendices. Chapter one is an introduction to the general research topics of tropical deer ecology and subsistence hunting as well as a major description of the study area. Chapter two describes the abundance, population structure and habitat use of the three species of deer. In this chapter several novel comparative techniques, such as the use of the cementum annuli histological technique used to age the skulls of deer hunted by local people were applied for the first time in a tropical deer community. The assessment of habitat use with a combination of GIS/GPS and participatory research techniques is also presented. Chapter three deals with a detailed quantitative description of the diet of deer studied from the analysis of stomach contents from hunted individuals and provides a detailed comparative analysis of the diet and the availability of food for the deer populations as assessed by a year-long quantitative phenological study of the major plant components in the diet. The possible role of two important species of plants in the diet of deer as potential Keystone Plant Resources (KPR) is discussed. Chapter four address a spatial and temporal analysis of the patterns of subsistence hunting of tropical deer populations and provides a novel approach for estimating the impact of human harvesting in wildlife populations from a spatial and temporal landscape perspective. Chapter five provides a general discussion of the thesis and also provides with possible management alternatives for both deer populations and subsistence hunting. Appendix I comprises a major literature review and analysis of the distribution and conservation status of the 18 species of deer in Latin America. This appendix is indeed a reprint of the first published product of this thesis in the form of an article in the journal *Ecoscience* (2.4 ISI impact factor in May 2004). Appendic II provides a comprehensive list of all plants composing the diet of the three species of deer and finally; Appendix III provides a detailed list of all hunting and sighting observations collected during field work as grouped by category and area.

CHAPTER TWO

Abundance, population structure and habitat use of sympatric deer populations in a tropical forest

2.1. Introduction

2.1.1. The evolution of ecological specialization

The evolution of ecological specialization and the concepts of "niche breadth" and "niche width" were popular topics of the ecological literature in the 1970s (Futuyma and Moreno, 1988). More recently, ecologist shifted their interest to study the evolution of coexistence of specialist and generalist species (Van Tienderen, 1997). Species are often faced with an evolutionary trade-off between performing a few activities well (specialists) or many activities poorly (generalists) (Wilson and Yoshimura, 1994). This trade-off is central concern to biologists interested in the coexistence of sympatric species (Wywialowski, 1987; Van Tienderen, 1997).

The use of multiple resources allows for partitioning, resulting in niche differentiation and coexistence (Krebs, 1994). Within a community or guild, niche differentiation occurs along several dimensions to facilitate coexistence. The number of dimensions increases with species richness (Krebs 1994; Futuyma and Moreno, 1988). Besides invertebrates, amphibians, reptiles, birds and small mammals (Bagchi *et al.*, 2003) niche separation and the evolution of coexistence has also been studied in ungulates. However, this has been dominated by research in temperate environments and the African savannas (Caughley and Sinclair; 1994; Geist, 1998). Little is known for tropical species, and even less for small forest-dwelling ungulates.

The ecology and behaviour of small, forest-dwelling ungulates is of interest also, because they are phylogenetically conservative, the current representatives of ancient lineages, and as such give some clues on how the ancestors of present day ungulates lived (MacCullough *et al.*, 2000). Many small forest-dwelling ungulates are solitary species and many more live in relatively large community groups (Geist, 1998).

While this concept had been thoroughly studied in a wide variety of taxa (Wilson and Yoshimura, 1994), there are very few publications on the evolution of specialist and generalist in tropical ungulates.

In India, Bagchi *et al.* (2003) studied the niche separation of two large cervids (*Axis axis* and *Sambar unicolor*) and two bovids (*Boselaphus tragocamelus* and *Gazella bennetti*) by analysing habitat use patterns and diet. These authors found clear niche separation between the two cervids, and competition between the two bovids in both habitat selection and diet preferences.

2.1.2. Deer in neotropical forests

Deer of the genus *Mazama* are the most abundant and widespread cervids in the tropical forests of America (Eisenberg and Redford 1999; Weber and Gonzalez, 2003). Eight species of *Mazama* have been recognized so far and *M. americana* and *M. gouasoubira* are by far the two most common and widespread species in the whole of Latin America (Weber and Gonzalez, 2003; Appendix I).

Mazama pandora is a recently re-discovered species from the Yucatan Peninsula in Mexico (Medellin *et al.*, 1998) but little is know of its ecology and distributional range. It was previously considered to be a subspecies of the red brocket deer (*M. americana*) by various authors or as the grey brocket deer (*M. gouasoubira*) by others. However, a recent study found that the species is clearly different in several anatomical traits from *M. americana* and *M. gouasoubira* and was re-named as *Mazama pandora* (Medellin *et al.*, 1998).

The few studies conducted on the ecology of the genus *Mazama* have focused largely on *M. americana* and *M. gouasoubira.* The feeding habits and some aspects of the reproductive biology of *M. gouasoubira* had been studied in Paraguay (Stallings 1984, 1986). One of the most extensive studies on *Mazama* population densities, feeding habits and genetics of the red brocket deer (*M. americana*) was developed in Suriname (Branan *et al.*, 1986; Smith *et al.*, 1986; Branan and Marchinton, 1987). Some aspects of reproduction, feeding habits, and population densities were studied in northern Venezuela (Bisbal, 1994). More recently, the feeding habits, population densities, age structure and productivity of *M. americana* and *M. gouasaoubira* have been studied in the Amazonian forest of northern Peru (Bodmer, 1989, 1991; Bodmer *et al.*, 2000; Hurtado-Gonzalez and Bodmer, 2003).

The white-tailed deer (*Odocoileus virginianus*) is another common deer species in the Americas that often shares the habitat with one or several brocket deer species (Weber and Gonzalez, 2003). Considerable research relating to the ecology of the white-tailed deer has been conducted in northern Mexico and Costa Rica mostly within temperate environments (i.e. oak-pine forest) and dry deciduous tropical forests (Rodriguez and Vaughan, 1994; Mandujano and Gallina,1995; Galindo-Leal and Weber 1998). Very little research on the ecology of white-tailed deer has been conducted in wet tropical forests. There have been no studies in Mexico concerning the ecology of the two *Mazama* species existing in the country.

Even when they are one of the most studied, abundant and widespread ungulates, the role of deer in tropical ecosystems is not yet well understood. Deer are important browsers in neo-tropical forests and many species (largely from the genus *Mazama sp.)* are frugivorous, consuming large amounts of seeds and fruits in a variety of forest and shrub-lands (Bodmer, 1989). Research has shown that deer are important seed predators of several species of palms and trees (Hoffman,1985; Branan *et al.*, 1985; Bodmer, 1989, 1991; Bisbal 1991). In addition, some deer species (mostly from the genus *Mazama*) might also act as seed dispersers for some plants (Bodmer, 1991). Deer are the major prey species of some of the top predators in tropical forests such as the puma (*Puma concolor*) and jaguar (*Panthera onca*) but the intricate predator-prey relationships between them are almost unknown in tropical ecosystems (Leopold, 1959; Eisenberg, 1989). Finally, the effects of deer browsing, seed predation and dispersal may have strong indirect effects on other trophic levels, such as the passerine bird communities that benefit from structured under-story vegetation for their foraging activities (Waller & Alverson 1997). All this, in turn, might have a strong effect on forest structure, composition and function where deer populations may play an important role. To date, no studies have specifically addressed the evolution of coexistence in the *Mazama* genus.

Recent studies in Latin America have demonstrated that subsistence hunting is still a major activity for rural human populations (Escamilla *et al.*, 2000; Peres, 2000, Robinson and Bennett, 2000; Mena *et al.*, 2000; Hurtado-Gonzalez and Bodmer, 2004). Together with peccaries (*Tayassu* spp.) and some large caviomorph rodents (e. g. *Agouti* spp.), deer are among the most preferred targets of these hunters (Peres, 2000; Hurtado-

Gonzalez and Bodmer 2004). In fact, deer are considered to be one of the most important sources of animal protein in rural Latin America (Hurtado-Gonzalez and Bodmer 2004). Finally, deer are also an important cultural component of the folklore, religion and regional traditions of many indigenous groups. These people regard deer as a totemic animal, a symbol of beauty, strength, speed or inspiration (Mandujando and Rico-Gray 1991; Galindo-Leal and Weber, 1998).

2.1.3. Technical difficulties for the study of tropical deer populations

From the logistical point of view, research on sympatric species of forest-dwelling deer is faced with a number of problems. Most species are solitary and live in remote, isolated regions; usually pristine and inaccessible habitats. The use of standardised techniques for the study of temperate deer can be inadequate in most cases. For example, the use of radio-telemetry to study habitat use of tropical deer species can be difficult, costly and time consuming (MacCullough *et al.,* 2000, Aung *et al.*, 2001). The use of distance sampling methods (e. g. population estimations in transects with support from the software DISTANCE) might be complicated, as many species are wary and rarely seen in some tropical forests (Carrillo *et al.*, 2000).

Nevertheless, a number of techniques had been developed and can be used for the study of tropical deer populations. For example; population estimations can be assessed with the use of indices of relative abundance (McGaffery, 1976; Mandujano and Gallina, 1995; Reby *et al.*, 1998; Carrillo *et al.*, 2000; Mayle *et al.,* 2000). Habitat use can be assessed with the use of indirect counts of pellet groups, track counts or deer vocalizations (Reby *et al.*, 1998; MacCullough *et al.*, 2000; MacShea *et al.*, 2001, Plumtre, 2000; Marquez *et al.*, 2001) and the use of hunting information can yield useful data on diet, habitat use and population age structure (Marks, 1994; Bodmer, 1991; 1995; Hurtado-Gonzalez and Bodmer, 2004). More recently the development of GIS (Geographic Information Systems) and GPS (Global Positioning Systems) technologies reveal many more possibilities for the study of tropical deer populations in tropical environments (Millspaugh, *et al.*, 2000; Radeloff, 1996., 1999; Broseth and Pedersen, 2000).

Furthermore, some of these technical difficulties for the study of deer populations were experienced during the development of this project in the GCR. From 1997 to 1999 we

engaged in a intensive attempt to capture, radio-collar and monitor deer in a forested section of the Nuevo Becal community. During this period and after more than 8,000 effective man/hours of trapping and capture effort with different methods (including net drives, modified snares and anaesthetic darting); only six deer (two males and two females *Mazama pandora* and one male and one female *Mazama americana*) were captured. No white-tailed deer were trapped although they were darted (with a combination of Xilacine and Ketamine hidrochloride) in two occasions, but they were never found in the dense thickets they run into afterwards. On the fate of the animals trapped, two died from post-capture stress and myopathy soon after capture. Two died from unknown natural causes (but likely from predation or hunting) three or four weeks after radio-collaring and releasing them, one radio-signal was lost probably as a result of battery failure or because the animal was hunted and the radio taken away or destroyed by the hunter and, finally; only one animal lived long enough and remained in the area for several months. Monitoring this single animal proved to be highly expensive and not technically/scientifically worth it and was interrupted after three months among other reasons because of lack of funding.

Very few studies have previously attempted radio-telemetry of deer in tropical forests. MacCullough's *et al.* (2000) study of wild Muntjac (*Muntiacus reevesi*) in Taiwan and Aung's *et al.* (2001) study of Elds deer (*Cervus eldii*) in Myanmar are two exceptions. Both obtained international support for expert technical and long-term financial assistance. Both were directed by recognized world authorities in deer population studies and yet, both deal with small samples sizes and little capture success. No study with radio-telemetry of any wild ungulate have been ever attempted in the Yucatan Peninsula (or elsewhere in Mesoamerica) in part because the forest structure and composition amid almost impenetrable thickets and seasonal flooding forests discourage the use of this technique for obvious reasons. Among the logistic limitations for this kind of studies in the area, the most important are the lack of radio-signal (because of closed tree canopy covers), complicated logistics for the capture and retrieval of captured animals and high post-capture mortality as a result of inefficient capture methods, predation and illegal hunting. Naranjo (2002) also attempted capturing and radio-collaring deer and other ungulates in the Montes Azules Biosphere Reserve, Chiapas, Mexico with very little success.

Future radio-telemetry studies in these tropical areas of Mesoamerica are encouraged to find international expert advice, ensure long-term financial assistance and experiment with different capture methods (perhaps using radio-tagged immobilising darts) to find the better alternatives for capturing and retrieving the elusive *Mazama* deer (and other ungulates) in the thick forests of the Yucatan Peninsula. Fore all the above reasons and the logistical difficulties involved in using them, the use of modern, more sophisticated techniques for the study of wildlife, is sometimes precluded in Latin America. The selection of methods used in the present study were among the only alternatives available for the study of deer populations in this area.

2.2. Chapter aims

Since very little is known of the ecological relationships among sympatric populations of tropical deer, this study attempt to investigate these relationships within a tropical forest region of the Yucatan Peninsula of Mexico: the Greater Calakmul Region, Campeche, Mexico (GCR). Here, the opportunity to study three species of deer living in the same habitat mosaic is unique, not only for Mexico, but for the whole of Mesoamerica and north of South-America, where deer diversity is regionally unique (Weber and Gonzalez, 2003).

The use of hunter-gathered information and cooperation for obtaining the exact geographical coordinate GPS positions of deer killing sites is developed and proposed here as a method to estimate habitat use patterns at a primary level. Adjustments and comparisons of other well known techniques such as the use of deer sign counts in transects for estimations of relative abundance, the tooth wear and replacement technique and the use of tooth cementum (dentin) annuli counts for age determination in deer is also presented for the first time for the Mexican brocket deer species.

This chapter presents one of the first comprehensive studies on the population and community ecology of three sympatric species of deer in Latin America; the red brocket deer (*Mazama. americana*) the Yucatan brown brocket deer (*Mazama pandora*) and the white-tailed deer (*Odocoileus virginianus*). The aims of this study were three-fold: (1) to document the basic population ecology (distribution, abundance, population densities, age and sex structure and habitat use) of sympatric populations of these three species of deer, (2) to provide practical ecological knowledge on the natural history of deer that can be used for conservation and management purposes in the GCR, and (3) to discuss the results obtained in this study within the framework of the theory of ecological specialization (Futuyma and Moreno, 1988) in the evolution of the *Mazama* genus.

2.3. Methods

2.3.1.Population estimations

Abundance

Deer population size estimates were conducted in two ways: (1) by the use of permanent transects designed for detecting changes in population trends through time. These transects were monitored monthly for a period of five years in selected areas that differed in their *a priori* characterization of hunting pressure and, (2) by means of temporary transects designed for detecting changes in the abundance of deer at different spatial scales. These were scattered in a larger area covering a wider range of habitat types.

From June 1996 to June 1999, and then again from March 2001 to January 2002, six permanent transects were monitored. These were located in three sites categorized *a priori* as heavily hunted, slightly hunted and non-hunted (the protected area inside CBR). The *a priori* categorization was based on quantifiable indirect evidence of subsistence hunting systematically searched for in the two hunted areas (e. g. encounters with hunters, disposed shotgun shells, number of shots heard, hunting camps, hunting dogs sighted or heard) (Cullen *et al.*, 2000; Peres 2000) and the effect of isolation and inaccessibility, law enforcement and lack of hunting evidence in the no hunted, protected area. The two hunted areas differed in the amount of evidence of hunting found, in at least an order of magnitude (e.g. 10 discarded shotgun shells found in the heavily hunted area while just one found in the lightly hunted area and similarly for the other parameters).

The permanent transects were 3 km long pathways (approximately 1.5 m width) cleared throughout the forest in locations where topography, soil conditions and understory/overstory conditions permitted comparison between sites with minor differences in habitat type. Length of the transect and location was chosen to attain maximum control on the effect of habitat differences in order to isolate the possible effects of hunting on deer density estimations (Peres, 2000). The transects were sampled at slow pace (about 1.2 km/h) during the first hours of daylight (usually between 07.00-10.00 am) at monthly intervals. The transects required clearing the understory vegetation at least twice a year for a clearer recording of deer tracks and pathways. After each cleaning, transects were left to "rest" for at least two weeks before sampling

in order to allow wildlife to return after the disturbance. A total of 1432 km were walked throughout this period of systematic monitoring of these permanent transects.

Between March 2001 and February 2002, 23 additional non-permanent transects were cut in locations different from the permanent ones to allow comparison in time and space of the two techniques (deer sightings and track/pathway counts), as well as between permanent and temporal transects. These transects were located randomly in forested areas in the same localities categorized as heavily hunted, slightly hunted and no hunted (protected area). To allocate these transects in a random fashion, dust roads and old abandoned logging roads (widely available in the study area in the form of grids) were located running north-south in INEGI (Mexico's Land Survey government office) maps. Using either a pace odometer (distance readings verified against exact known distances in flat terrain obtained with +/- 10 meters of error) whilst walking on the logging roads or using the odometer of a four-wheel drive vehicle, the total distance of the road was measured and numbered in sections using kilometres or hundreds of meters. The location of the transects were then chosen using the first two random numbers generated with a pocket calculator and starting the transect perpendicular to the road (normally with an east-west bearing) and with the help of a hand-held compass. According with terrain accessibility, these transects were from 3 to 5 (mean 3.8) kilometres long. Both deer sightings and deer tracks and pathway in the form of evident deer trails (Mayle *et al.*, 2000) counts were recorded in the same fashion as in the permanent transects and accounted for a total of 128 km of censuses. Both temporal and permanent transects were measured with a hip thread chain and marked every 100 meters with flagging tape (Figure 2.1).

Estimation of relative abundance is reported as "Sign Encounter Rate" (SER) calculated as the number of signs (deer tracks and pathways, visual observations when species, sex and age was possible) observed and recorded in a given length of transects (e.g. tracks/km). The tracks of white-tailed deer are from 1.5 to 2 times larger than those of brocket deer and easy distinguishable from those of the smaller *Mazama* species (Aranda 1981). The tracks of both brocket deer species were pooled as it was not possible to distinguish between them. Tracks of young white-tailed deer potentially overlapping the size of the *Mazama* spp. are normally associated with the tracks of an adult deer, usually the nursing female. Clumped sets of tracks were considered as from

one individual and are not to be confused with the count of deer pathways as these might belong to more than one deer but were counted as single sighting events (Mayle *et al.*, 2000) This method is now standard for the analysis of spatial and temporal trends in the abundance of wildlife populations, where the use of more sophisticated methods is precluded by habitat variables or other traits (McGaffery, 1976; Escamilla *et al.*, 2000; Carrillo *et al.*, 2000; Mayle *et al.*, 2000).

To explore the relationship between deer abundance (SER/km) and the straight-line distance between the temporary census transects and the Nuevo Becal Village, these distances where measured using the GIS and Spearman rank correlation coefficients where calculated to test the hypothesis that deer abundance decreased as distance to the Nuevo Becal village increased.

Density estimations.

In additional to the estimation of abundance using SER, densities of white-tailed deer and brocket deer were estimated with standard line transects methods (Buckland *et al.*, 1993). The fixed width transect method (Lancia *et al.*, 1994) was utilized where the standard visibility strip was defined as 30 meters. Visibility was fixed at 30 meters because heavy understory vegetation in most habitats did not allows assessment of species sighted at distances greater than this. Distance sampling using the software DISTANCE 3.5 (Thomas *et al.* 1998) was employed to obtain density estimations of deer observed where it was possible to accurately measure perpendicular distances to the centre line of the transect (Buckland *et al.*, 1993). Perpendicular distances were measured with a plastic 50 meters measuring tape. A minimum of 20 records (sightings) are needed if the observations are to be considered unbiased (Buckland *et al.*, 1993). Therefore, only data coming from the temporary transects surveys were used in density estimations, because data from permanent transects does not meet the criteria of transect stratification, randomness and observer independence. Moreover, very few sightings of deer where recorded in permanent transects during the course of the main SER sampling period (1996-1999). SER provided temporal and spatial indices of abundance among sites with different hunting pressures and different habitats (e.g. forest types) while density estimations where mainly used for testing the accuracy of the SER estimates and for comparisons with other studies in other Neotropical forests. Additionally, the mean

group size of deer was estimated by averaging the number of observations when one, two or more individuals were seen together.

2.3.2. Population sex and age structure

Deer skulls were collected with the cooperation of participating hunters. The skulls were prepared in the field (by the hunters themselves) or in the laboratory by washing and soaking them in soapy hot (90° C) water. The fourth premolar (PM4) was extracted from the skull for cementum annuli (dentine ring) aging. Samples were sent to a recognized laboratory for cementum ring aging (Matson's Wildlife Laboratory, P. O. Box 308 Milltown, Montana 59851 USA, www.matsonslab.com). This laboratory has more than 30 years experience in age determination of a variety of wildlife species in America, including two of the three deer species studied here (*Odocoileus virginianus* and *Mazama americana*). We tested the hypothesis that brocket deer and white-tailed deer from the study area have similar cementum annuli patterns from those of white-tailed deer elsewhere in North America.

The fourth premolar (PM4) was chosen for histological analysis of cementum annuli deposition, because most skulls frequently lack the incisor teeth most commonly used for age determination with this technique. A few adjustments to the technique such as knowing the exact culling date were necessary to accurately age the skulls of *Mazama* species. Skulls of very young deer (< 1 year old to 1.5 years old) that had clear incisor eruption patterns and no missing teeth were used to assess the reliability of the technique in the absence of known-age individuals (Matson's Laboratory, Miltown Montana, USA, personal communication, 1999). Seventy-eight tooth samples from a total of 219 skulls examined (152 skulls collected in the present study and 67 deer skulls collected in the past by other researches and deposited in the Zoology Museum of El Colegio de la Frontera Sur (ECOSUR), Chetumal, Quintana Roo, Mexico) were sent for cementum-aging analysis while the rest were aged using the tooth wear technique widely used for aging white-tailed deer in North-America (Severinghaus, 1949). Close-up high resolution digital photographs were taken of every skull and mandible to develop a deer skull catalogue for further comparisons of the two techniques. The complete skull collection was deposited in the Zoology Museum of El Colegio de la Frontera Sur (ECOSUR) Chetumal, Mexico reference number eco/zma/2348-99.

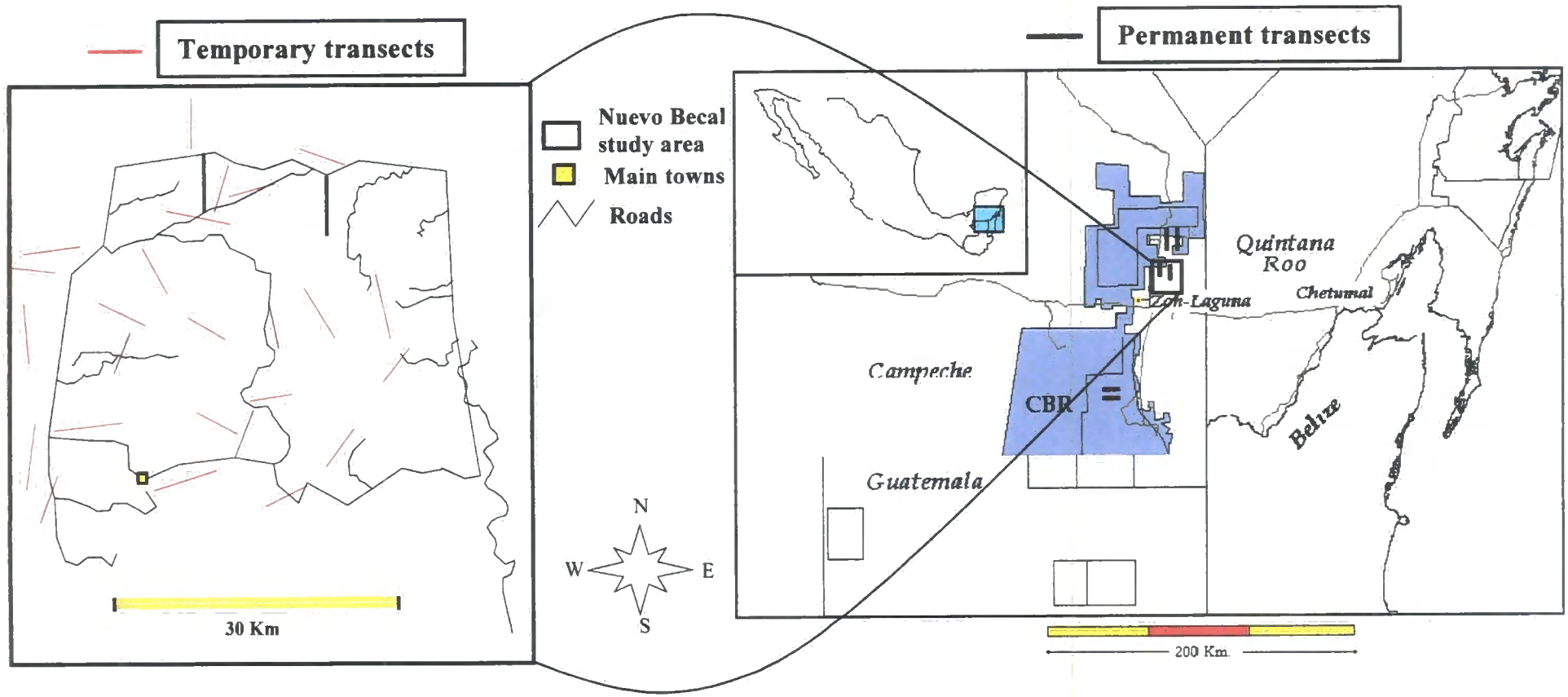

Figure 2.1. Stratified random location of the transects used for estimation of deer abundance, density and for characterization of forest structure and composition. The map show the geo-referenced location of each transect in relation with major roads and trails in the study area, Nuevo Becal, Calakmul Region, Campeche, Mexico.

Aging whitetail deer by tooth replacement and wear is nearly 100% accurate for deer of ages 0.5, 1.5, 2.5, and 3.5+ years (Williams *et al.* 2001). After 3 years, wear rather than eruption of new teeth are used for aging and the technique become less reliable (Hamlin *et al.* 2000). Research shows that "field aging" (tooth replacement and wear) is more accurate than cementum annuli for deer 3.5 and younger (Hamlin *et al.*, 2000). For older deer, the cementum annuli technique provides better results. There can be variability between observers on the same deer, but for management purposes, field aging is a very useful tool (Severinghaus 1949). Tooth eruption and wear patterns were estimated and recorded with known age specimens (cementum annuli aged skulls) against unknown aged specimens. Cross comparisons of the two techniques were performed by asking 3 trained volunteers to "field age" the skulls using the photographic skull catalogue and the percentage of accuracy (by matching ages) with each technique was then estimated.

When the two techniques had been standardized, deer ages were used to construct life tables to allow population age structure assessment. Life tables were constructed following the stable age distribution method (Caughley, 1978) pooling skulls of all three deer species together because of the large sample size required for this method (stable age distribution life tables cannot be constructed with samples smaller than c. 100). For the purposes of this study, pooling the three species together is a considerable compromise, precluding the evaluation of age structures by species with this method. However, since one of the main interests of this study was the assessment of the effect of hunting on the whole deer community at a fine scale (see Chapter 4), this compromise might be considered acceptable for certain management purposes. Stable age distribution life tables provide age-specific mortality rates at cohort intervals (Caughley, 1978). The smaller the age class, the higher the precision on the survival and mortality rates (Caughley 1978; Udevits and Ballachey 1998). The method used assumes that the number of animals aged x in a standing population is compared with the number of these that subsequently died before attaining age $x + 1$ (Eberhardt, 1969). Survivorship curves (lx) can be later estimated for individual deer species. Finally, the method of deer aging using the combination of cementum rings and tooth replacement and wear was compared with that used by Hurtado-Gonzalez and Bodmer (2004) to age brocket deer in the Peruvian Amazon. Survival rate curves were used for these comparisons.

2.3.3. Habitat Use

Habitat use was estimated using all records of deer sightings for which a GPS position was obtained during formal transect surveys and opportunistic observation of deer in other visits to the forest. GPS positions of deer killed by hunters in different habitat types were obtained for evaluation of hunting pressure (Chapter 4) and were also included within the data set. GPS coordinates were obtained using a Trimble II Geo-Explorer hand-held GPS receiver (Trimble Inc., Palo Alto, California) and later a Garmin e-Trex GPS, (Garmin Corp. Olathe, Kansas). According with these manufacturers, both units have similar accuracies of around 3 to 5 meters (even in forested habitats) when satellite reception is more than four satellites for non differentially-corrected data. No attempt was made to perform differential correction of the GPS data, because the inherent error in the way hunting GPS records were recorded was larger than the non-differentially corrected error. The coordinates of deer killings and sightings were later located in vegetation maps created from LANDSAT TM imagery (Martinez and Galindo-Leal 2003) (but see Chapter 3 for a detailed explanation of the development of the vegetation map used in this study). The five major vegetation types (Tall Evergreen forest, Lowland Flooding forest, Short Deciduous forest, Second growth vegetation areas and Agricultural areas) were used for the analysis of habitat use. A sixth vegetation type called "Deforested" was also used by adding the pixels of both Agricultural and Second growth vegetation areas together. When "Deforested" was used in any analysis, both Agriculture and Second growth vegetation areas were removed, and vice-versa.

Each GPS position was buffered using ArcView v3.2 Spatial Analyst (ESRI, Redlands, California) with buffers of 200 meter diameter. This diameter was used because; (1) the average error for a good satellite reception was estimated at 100 meters under closed forest canopies and (2) approximately the same distance (100 meters) was estimated as error to determine the exact deer killing (or carcass retrieving) point in some of the hunting records (see also Chapter 4 for more detailed information on GPS positions). The within-buffer composition of habitats was measured using ArcView Spatial Analyst (Figure 2.2). Ivlev's indices of selectivity (Krebs, 1989) were used to estimate habitat preferences or avoidances, using the mean values of surface cover of each vegetation class within the buffered points. Habitat availability was estimated as the proportion of each vegetation classification for the study area (155,000 ha) in the vegetation map. The

Ivlev's index ranges from −1 indicating avoidance to +1 indicating habitat preference (Krebs, 1989).

To look at differences in habitat composition within the buffered points, Kruskall-Wallis tests were performed for each vegetation type, because the data was not normally distributed (McShea *et al.*, 2001) precluding the use of a parametric ANOVA. A Mann-Whitney test was performed to look at differences in habitat use between sexes a ages of deer. A post-hoc multiple comparison (Dunn's) was performed to look at differences in the ANOVA mean rank values, this procedure does not allow selection for preferences and avoidance in habitat use values, because this will indicate statistical associations rather than actual animal preferences. (Zar, 1996; McShea *et al.*, 1991). Therefore, the Ivlev's indices were considered closer to real animal preferences (Krebs, 1989; McShea *et al.* 2001). The Shannon-Wiener index (Krebs, 1989) was calculated as a measure of habitat diversity for the within-buffer composition of habitat (vegetation) types, and compared between deer species and between dry and wet seasons. Serial autocorrelation of GPS points was considered non existent as the data is temporarily independent and each point represent an individual deer.

2.3.4. Statistical Analysis.

Whilst the majority of statistical analyses were performed using SPSS v.10 (SPSS Inc. Chicago, Illinois) for Windows, other programs were also used. For the analysis of the log-likelihood tests (G test), specific macros were built in Excel XP (Microsoft Corp. Seattle, Washington), since no commercial or shareware statistical software was available for this test. The advantage of the log-likelihood test is that in situations where expected proportions are not derived from field data (e.g. calculated expected frequencies), the test is more reliable than the chi square test (Dytam, 1999) All statistical analysis were performed following Zar (1986) and Dytam (1999).

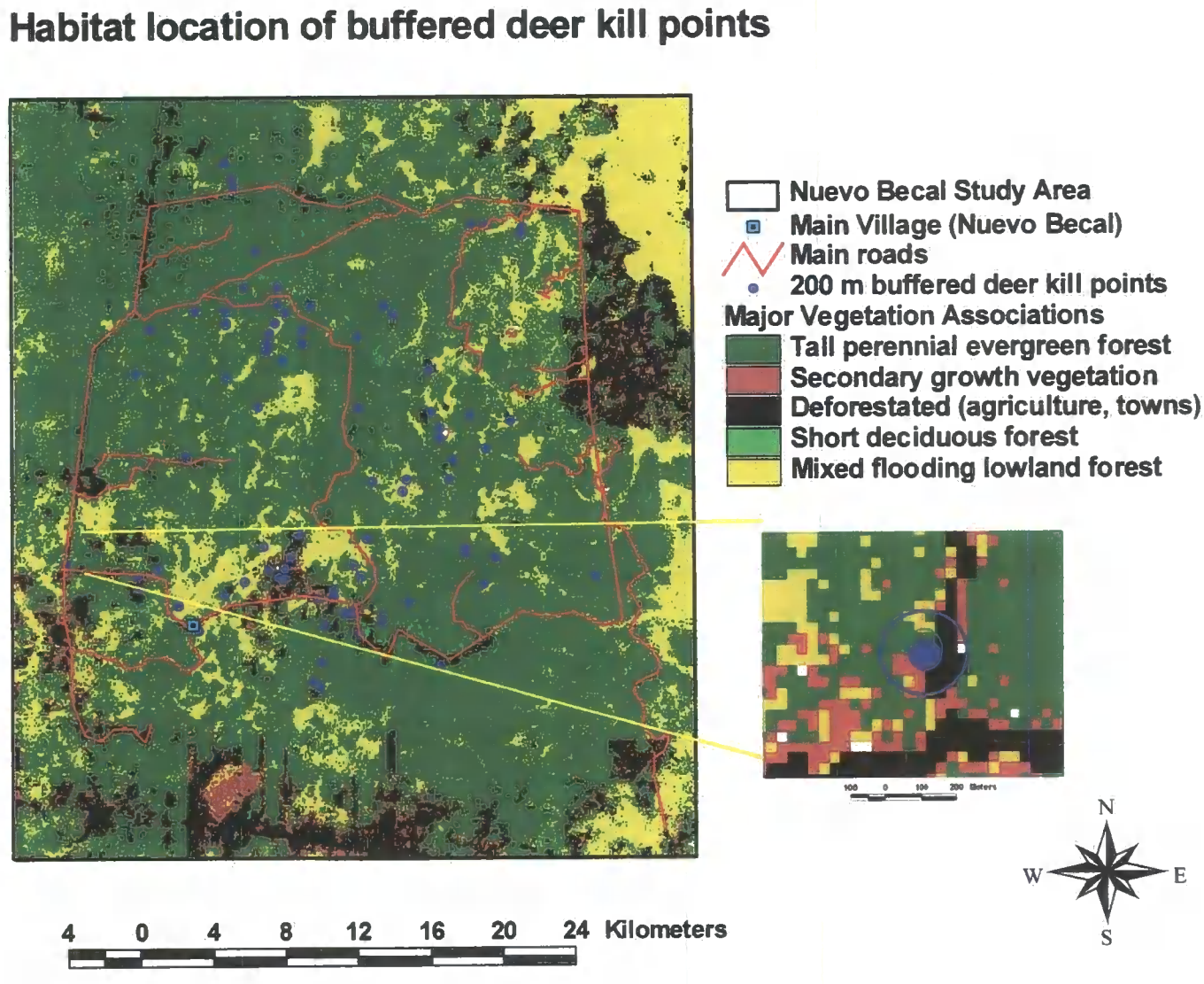

Figure 2.2. Location of both sighting and hunting GPS deer records in the study area. Blue coloured points represent buffers of 200 m diameter. The inset show the composition of vegetation classes of one of the buffered points.

2.4. Results

2.4.1. Population estimations

Abundance

The relative abundance of *Mazama* spp., as derived from sign encounter rate (SER) was from 1.2 to 6.5 times higher to that of *Odocoileus virginianus* (Figure 2.3). By comparing SER in the areas with different hunting pressure, it was found that the area with no hunting pressure had a similar abundance of white-tailed deer (1.7 signs/km) to that of the two brocket deer species pooled together (1.9 signs/km). The abundance of white-tailed deer in the heavily hunted area was ten-fold lower (from 1.7 to 0.09 signs/km) than that in the non-hunted area (Figure 2.3).

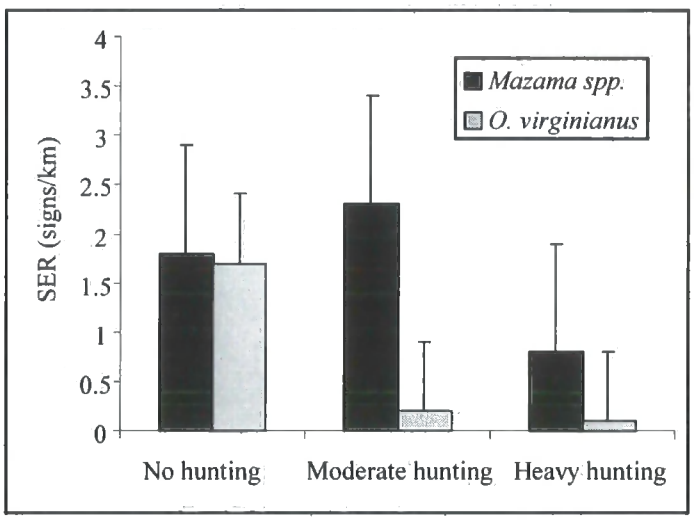

Figure 2.3. Relative abundance of *Mazama* spp. and *Odocoileus virginianus* in areas characterized *a priori* as having heavy, moderate and no hunting pressures. Error bars are one standard error of SER on spatially independent replicates (transects).

The abundance of white-tailed deer was very low in both temporary transects (0.018 signs/km) and permanent transects (0.009 signs/km), while the abundance of *Mazama* spp. was higher in permanent transects (Table 2.1). This difference was statistically significant for *Mazama* spp. ($G = 33.45$, d. f. = 2, $p < 0.001$) but not for the white-tailed deer (Figure 2.4).

The highest abundance of both white-tailed and brocket deer was found in the Tall evergreen forest, followed by the Short deciduous and Flooding lowland forest. These

differences were highly significant for both *Mazama* spp. and the white-tailed deer (G = 23.12, d. f. = 2, $p < 0.005$) (Figure 2.5).

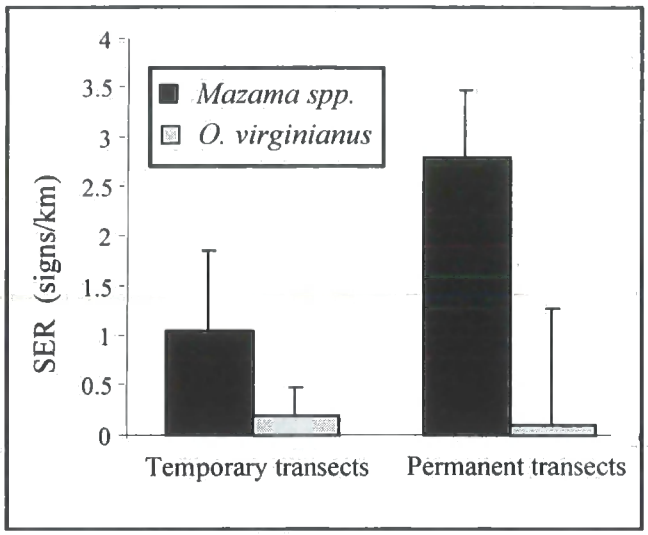

Figure 2.4. Relative abundance of *Mazama* spp. and *Odocoileus virginianus* in temporary transects monitored once during 2001 and permanent transects monitored monthly from 1996 to 2001. Error bars are one standard error of SER of spatially independent replicates (transects) on temporary transects and non-independent temporal replicates for permanent transects (possible pseudo-replication in the latter).

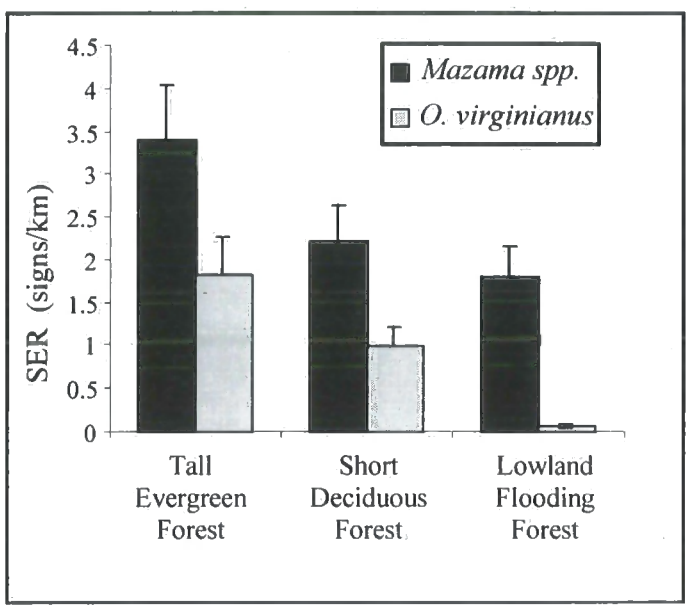

Figure 2.5. Relative abundance of *Mazama* spp. and *Odocoileus virginianus* in three main vegetation types. Data from temporary transects monitored once during 2001. Error bars are one standard error of SER of independent replicates (transects) on each vegetation type.

The monitoring of abundance trends from 1996 to 1999 and then again in 2001 show a clear, steady decline in the abundance of white-tailed deer to zero abundance (local extirpation) in 1999 and near zero (0.09 signs/km) in 2001. These differences between years were marginally significant (Kruskall-Wallis test, F = 11.03, d. f. = 4, p = 0.05 (Figure 2.6).

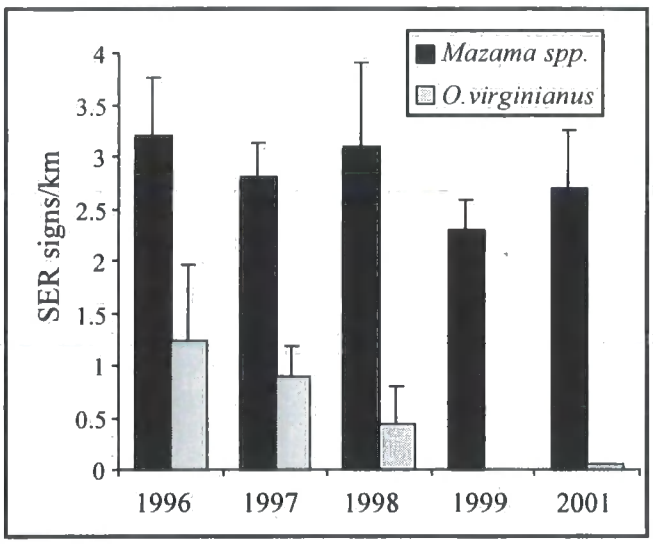

Figure 2.6. Trend in relative abundance of *Mazama* spp. and *Odocoileus virginianus* monitored monthly in permanent transects from 1996 to 1999. Error bars are one standard error of SER for non-independent temporal replicates on permanent transects (possible pseudo-replication).

In contrast to the above, the trend in the abundance of *Mazama* spp. appears to be stable with similar values throughout the years of the study, and the differences were not significant (Kruskall-Wallis test F = 9.32, d. f. = 4, p > 0.1) (Figure 2.6).

The relative abundance of *Mazama* spp. decreased in the transects sampled (n = 23) as straight-line distance to the Nuevo Becal village increased (Spearman rank correlation r = 0.87, df = 22, p < 0.001). No relationship exists for the white-tailed deer (Spearman rank correlation r = 0.43, df = 22, p > 0.05). However, when only those transects that contained either agriculture or deforested areas were analysed (n = 7), the abundance of *Odocoileus virginianus* increased as straight-line distance to Nuevo Becal increased (Spearman rank correlation r = 0.81, df = 6, p < 0.001) and again the abundance of *Mazama spp.* decreased as straight-line distance to the hunter's village increased (Spearman rank correlation r = 0.93, df = 6, p < 0.001) in this sub-set of transects.

Density

Density estimations using permanent transects also indicate a higher density of *Mazama* spp. (0.09 deer/km^2) than white-tailed deer (0.02 deer/km^2). The density estimations were almost two fold lower in temporary transects for both species (Table 2.1). Although comparisons of density estimates with those obtained from SER are not possible, because SER cannot be transformed to density estimates (deer/km^2), it is interesting to note that figures are proportionally similar for both *Mazama* spp. and the white-tailed deer. The mean group size of both *Mazama* spp. and *Odocoileus virginianus* was similar, with the majority of observations being of solitary individuals (Table 2.1).

Transect type	Abundance	Method	*Mazama* spp.	*Odocoileus virginianus*
Fixed permanent transects 1996-1999	Absolute	Density (± s. e) of deer/ km^2 obtained by distance sampling (program *Distance3.5*)	0.90 ± 0.72	0.021
	Relative	SER (± s. e) deer signs/km.	2.78 ± 0.68	0.009 ± 0.005
	Relative	Deer sighting rate (deer/km)	0.030	0.01
	Mean deer group size + (range)		1.02 (1-2)	1.42 (1-3)
Stratified-random temporary transects 2001	Absolute	Density (± s. e) of deer/ km^2 obtained by distance sampling (program *Distance 3.5*)	0.085 ± 0.063	0.009 ± 0.004
	Relative	SER (± s. e) deer signs/km.	1.03 ± 0.82	0.018
	Relative	Deer sighting rate (deer/km)	0.021	0.008
	Mean deer group size + (range)		1.02 (1-2)	1.12 (1-2)

Table 2.1. Comparison of results obtained with different deer abundance estimation methods for *Mazama spp.* and *Odocoileus virginianus,* in both permanent transects (used for monitoring deer population trends in time and space from 1996 to 1999) and temporary transects (used mostly for comparison of abundance in different habitat types during 2001).

2.4.2. Population sex and age structure

The analysis of cementum rings on molars of the two *Mazama* species and in tropical white-tailed deer demonstrate that the technique can be used to accurately assess the age of deer in the GCR. The percentage of matching age classifications by the three independent volunteers that assessed deer mandibles with the eruption and wear technique was up to 90%. No differences in accuracy of aging were noted among the three volunteers for the three species of deer. However, aging *Mazama americana* with the tooth eruption and wear technique was more difficult than aging *M. pandora* or *O. virginianus* because tooth wear patterns are less marked in this species and the percentage

of accuracy dropped to 70%. This can be related with dietary preferences in this species (but see Chapter 3).

No differences were found in cementum annuli deposition patterns between tropical white-tailed deer populations in the GCR and major white-tail populations in the USA (Matson Wildlife Laboratory report number GR-323/2000). The analysis of dentine ring deposition in the molars of the two *Mazama* species show that the technique is highly accurate after 1.5 years and up to 14 year of age with very similar tooth eruption and wear patterns to those of white-tailed deer. For animals whose age was estimated to be younger than 1.5 years old, their final age was easily assessed by the tooth eruption and wear technique. Skulls of *Mazama* of this age range (n = 6) with a lot of missing teeth were excluded from the analysis.

The life table show a typical ungulate mortality pattern characterized by a high mortality rate of juvenile deer at the ages of 1 and 2 years old and a more stable mortality rate in all other cohorts. The fact that mature individuals of ages 10, 12, and even 14 years old were detected, is an indicator of the health of the population suggesting that deer are probably not being over-harvested at current harvest rates (Table 2.2).

Age	**Frequency (rounded)**	**Survival**	**Mortality**	**Mortality rate**	**Survival rate**
X	***fx***	***lx***	***dx***	***qx***	***px***
1	67	1	0.418	0.418	0.582
2	39	0.582	0.329	0.565	0.435
3	17	0.253	0.056	0.220	0.780
4	13	0.197	0.108	0.548	0.452
5	6	0.089	0.030	0.330	0.670
8	4	0.059	0.015	0.254	0.746
10	3	0.044	0	0	1
14	3	0.044	0	0	1

Table 2.2. Stable age distribution life table of ages estimated from skulls (n = 152) of the two brocket deer (*Mazama americana* and *M. pandora*) and white-tailed deer (*Odocoileus virginianus*) collected from 1996 to 2001 in the GCR, Mexico. Calculations after Caughley and Sinclair (1994).

In general, there were more males of *Mazama americana* harvested than females (t = 3.24, d. f = 2, p < 0.005). No statistical differences were found between the sex ratios of the other two species (Figure 2.6). There were no differences in sex ratios in the age

classes assessed within 1 year intervals on the three species of deer harvested (Figure 2.7). In contrast, differences were observed in sex ratios for "fawn, juvenile and adult" age classes (Figure 2.8). There were significantly more juveniles *Mazama americana* harvested than fawns and adults (Man-Whitney test, $U = 67.4$, d. $f = 2$, $p < 0.05$) (Figure 2.9). No differences in sex ratio (at this age class classification) were detected on the other two species (Man-Whitney test, *M. pandora* $U = 12.34$, d. $f = 2$, $p > 0.1$; *Odocoileus virginianus* $U = 17.42$, d. $f=2$, $p > 0.5$) (Figure 2.8 and 2.10).

By comparing the method of age classification used by Hurtado-Gonzalez and Bodmer (2004) (hereafter referred to this as Bodmer's method) that uses just four age classes divided by two years intervals with the more precise aging technique of cementum annuli, it can be noted that the resulting survival curves from the cementum annuli technique (Figure 2.11) are smoother and closer to a normal distribution. Data obtained using this method, hence did not require logarithmic transformation.

While differences in survival rates among juvenile cohorts of *M. americana* and *M. pandora* (second age class) were encountered with the first method (Kolmogorov-Smirnov test $D = 2.24$, $p < 0.05$), there where no differences using the smoothed distribution obtained with the more accurate aging technique (K-S test, $D = 0.62$, $p > 0.1$). It was not possible to compare these two techniques for age structure classification in the white-tailed deer due to the small number of skulls available by cohort (Figure 2.10).

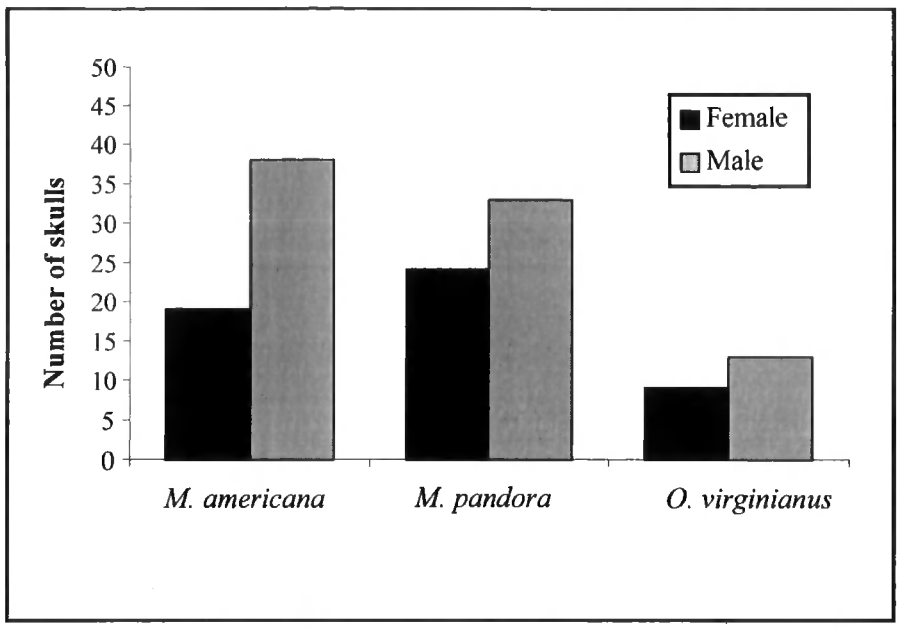

Figure 2.7. Population sex structure determined from skulls collected in this study (n = 152) of the red brocket deer (*Mazama americana*), Yucatan brocket (*Mazama pandora*) and white-tailed deer (*Odocoileus virginianus*) hunted in the GCR, Mexico from 1996 to 1999.

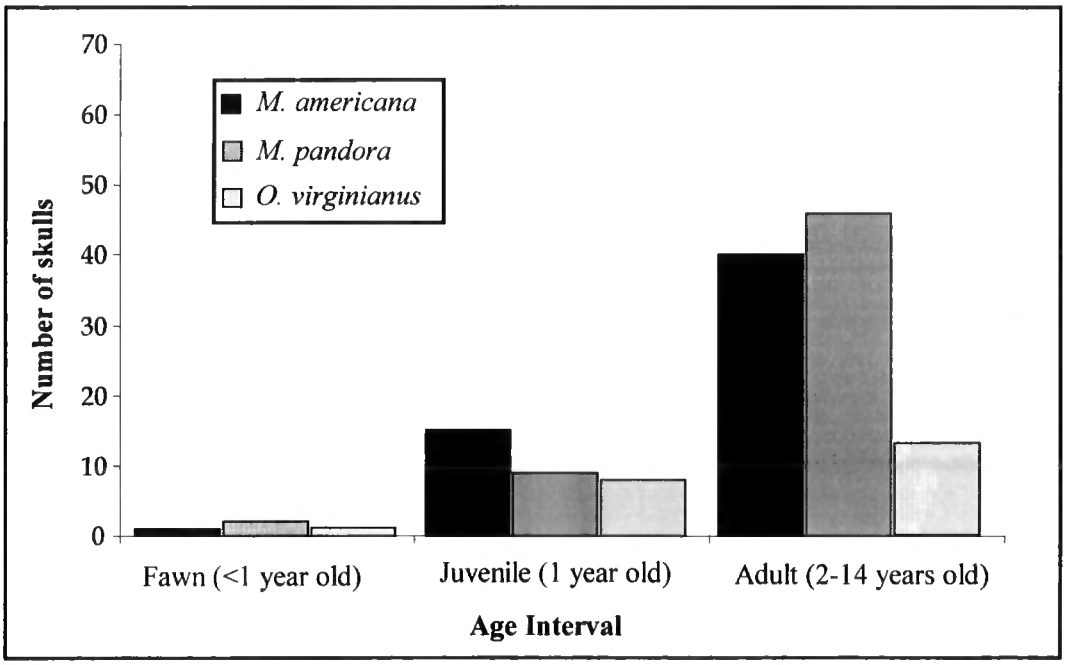

Figure 2.8. Population age structure by gross age classes determined by the tooth wear and replacement technique analysis of skulls (n = 152) of the red brocket deer (*Mazama americana*), Yucatan brocket (*Mazama pandora*) and white-tailed deer (*Odocoileus virginianus*) in the GCR, Mexico.

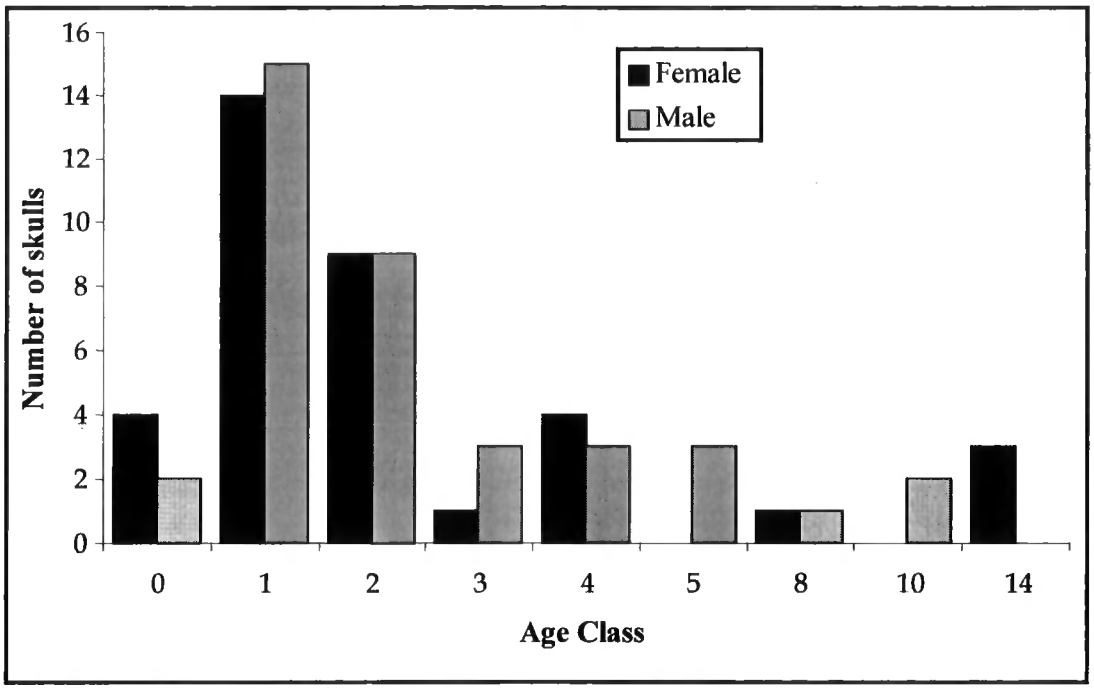

Figure 2.9. Population age structure in relation to sex ratio as determined by cementum annuli histological technique analyses of skulls (n = 78) of all deer species pooled together in the GCR, Mexico.

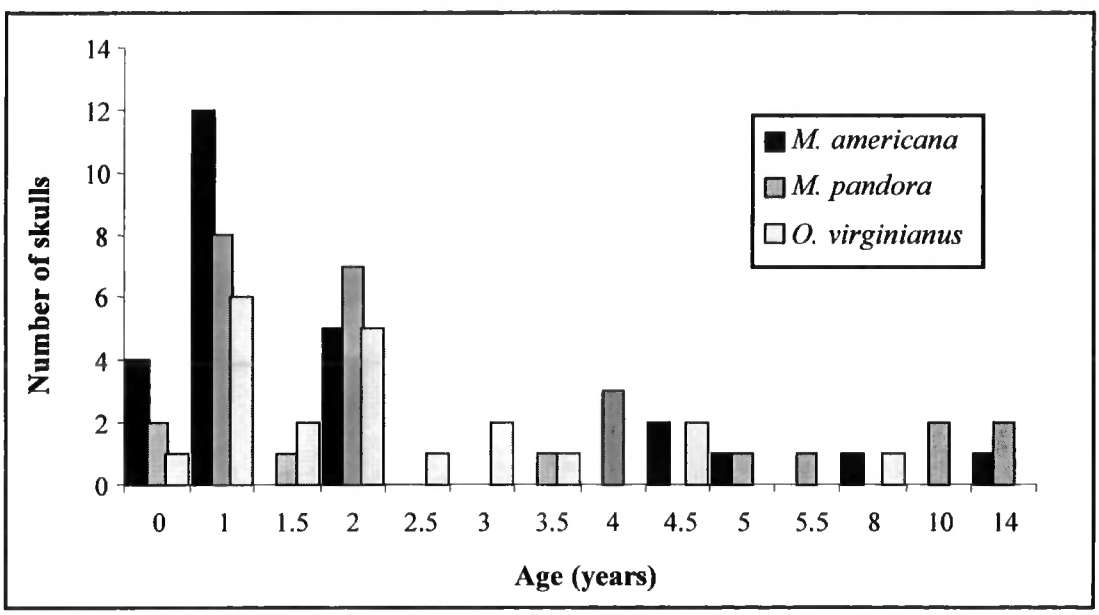

Figure 2.10. Population structure age classes determined by cementum annuli technique (n= 78) based on the analysis of teeth from skulls of the red brocket deer (*Mazama americana, n = 27*), Yucatan brocket (*Mazama pandora, n =28*) and white-tailed deer (*Odocoileus virginianus, n = 23*) in the GCR, Mexico.

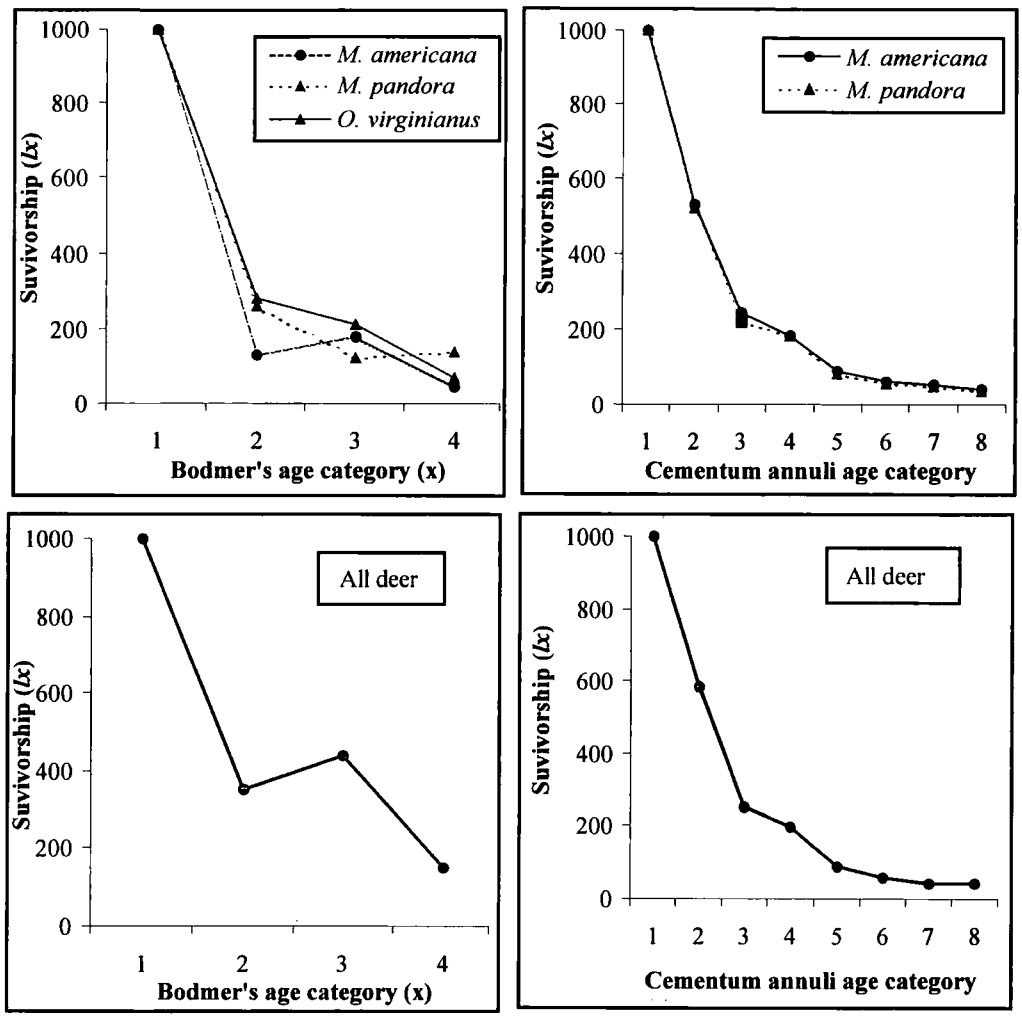

Figure 2.11. Survivorship curves from the age structure determined by gross age classes (n = 152, Bodmer's method, plots on the left) and fine age classes by cementum annuli histological technique (n = 78, plots on the right) of skulls from *Mazama americana*, *Mazama pandora* and *Odocoileus virginianus* in the GCR, Mexico. Calculations of survivorship are from Table 2.2 after Caughley and Sinclair (1994).

2.4.3. Habitat use

In general terms, the three species of deer used most habitat types in proportion to their relative availability according with Ivlev's index of selectivity (Table 2.5). The three species of deer had different habitat preferences in the study area and it appears that they are separated by different habitat use patterns and preferences.

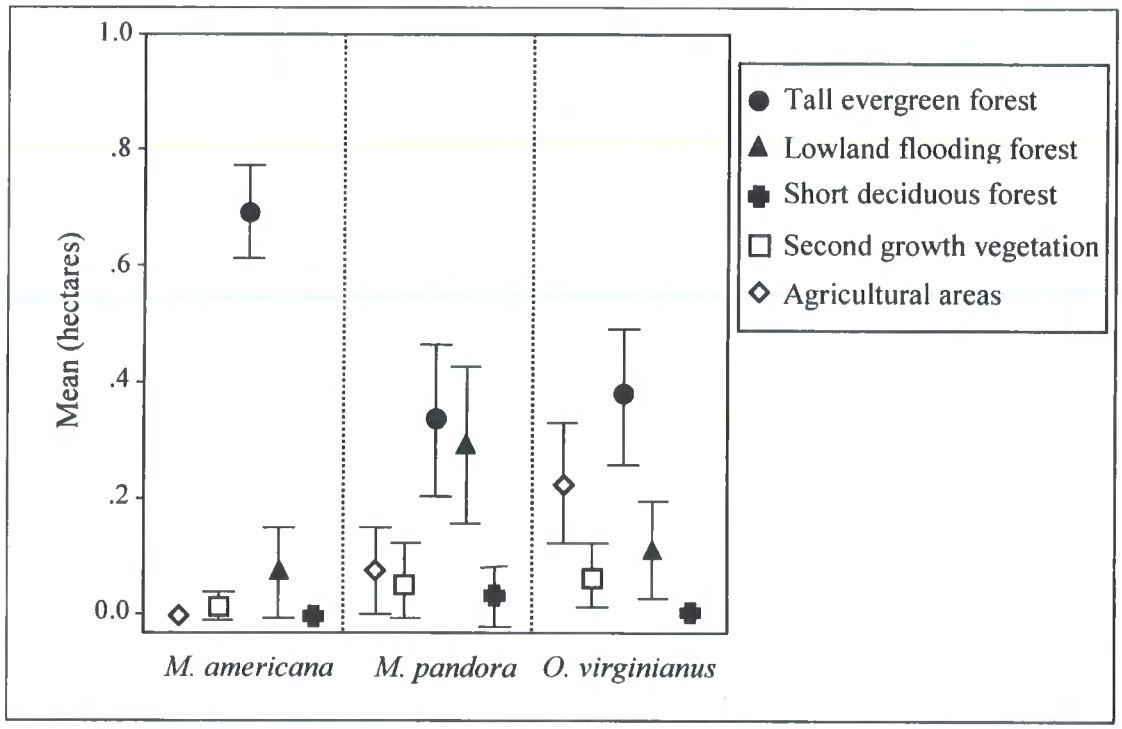

Figure 2.12. Habitat use of *Mazama americana*, *Mazama pandora* and *Odocoileus virginianus* in the GCR, Mexico. Values are mean (markers) and 95% confidence interval (whiskers) of total number of records (deer killings, transect sightings and opportunistic sightings) for which a GPS position was obtained.

The composition of habitats within buffers presented a distribution different from normal, therefore a Kruskall-Wallis non-parametric ANOVA was performed to test for differences in habitat use. Since this is a rank test (Zar 1996) a multiple comparison's test (Dunn's test) was performed in order to distinguish for the ranks responsible of the statistical differences between the three species of deer (Table 2.4) To look at differences by sex (male-female) or age classes (juvenile-adult) in habitat use, Mann-Whitney U tests were employed.

Most *Mazama americana* buffered points had a high proportion of the buffer surface (69%) covered by Tall Evergreen forest with lower proportions for all other vegetation types. Both the white-tailed deer and *M. pandora* had more even proportions in habitat compositions within the buffers. The Kruskall-Wallis test shows that these differences are highly significant for all but two habitat types (Short Deciduous forest and Secondary Growth vegetation)(Table 2.4, Figure 2.12).

Vegetation type *(2 degrees o freedom)*	**Kruskall-Wallis Mean rank values (hectares)**			**Test statistics**		
	Mazama americana (n = 27)	***Mazama pandora*** (n= 30)	***Odocoileus viginianus*** (n = 35)	***H***	***P* value**	**Sig.**
Agriculture	35.4[a]	44.37[a]	56.81[b]	17.8	p < 0.001	***
Secondary growth	40.0	47.08	51.10	5.02	p > 0.05	ns
Deforested	34.70[a]	46.23[a]	55.83[b]	14.0	p < 0.001	***
Tall evergreen forest	65.83[b]	36.20[a]	40.41[a]	21.6	p < 0.001	***
Flooding forest	37.50[a]	57.77[b]	43.79[a]	11.1	p < 0.005	**
Short deciduous forest	44.30	45.70	48.89	2.05	p > 0.1	ns
Unclassified pixels	0.202	0.088	0.000			

Table 2.3. Habitat composition inside buffers (mean values are hectares within 200 m diameter buffer) as recorded by deer sightings and culling site GPS positions in the habitat vegetation map (30 x 30 meters pixels). Kruskall-Wallis p values were considered as: *** = highly significant when $p < 0.001$, ** = marginally significant when $p < 0.01$ and n. s = non significant when $p > 0.05$ (see also individual habitat charts for confidence intervals). A multiple comparisons (Dunn's) ranks test (no adjustment for ties) was considered significant when $p < 0.05$ rated as different letters in the same row (i.e. when a and a = non significant). This test was not performed if the K-W test was not significant.

There were no differences in habitat use by sex (male-female) and age (juvenile-adult) classes for the three species of deer (Mann-Whitney tests, all d. f = 2, $p > 0.05$). This might have been the result of small sample sizes due to instances of missing data for sex or age categories in the GPS point data set. Therefore, this lack of statistical differences should not be taken at face value.

The highest diversity of vegetation types was calculated for the white-tailed deer points and the lowest was for *Mazama americana* points. *Mazama pandora* presented

intermediate values in diversity (Figure 2.13). These patterns were statistically significant (Wilcoxon paired test $z = 13.48$, $df = 1$, $p < 0.005$) for points obtained during the dry season, but not for points obtained during the wet season for the three species of deer (Figure 2.13). *Mazama americana* displayed strong preferences for the Tall Evergreen forest, and avoided Deforested areas and Agricultural vegetation types (Figure 2.15, table 2.4). The white-tailed deer preferred both the Agriculture and Deforested vegetation types

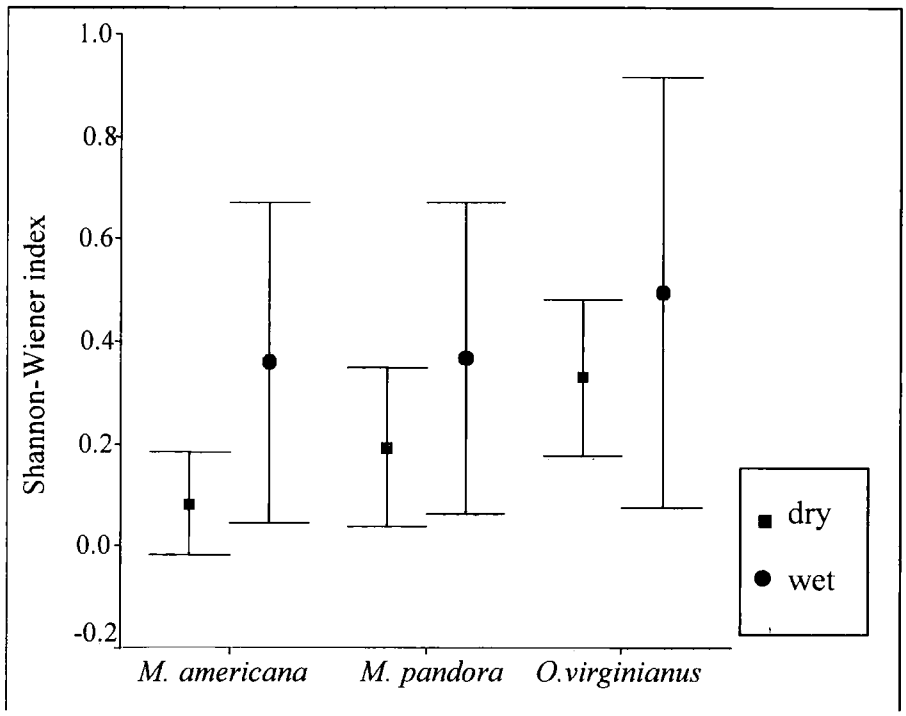

Figure 2.13. Mean and 95% confidence intervals of Shannon-Wienner diversity indices for all vegetation types contained within-buffered GPS positions of *Odocoileus virginianus*, *Mazama americana* ,and *Mazama pandora* during the wet and dry seasons.

Vegetation type (proportional availability)	Ivlev's index of selectivity values and habitat preference ranks		
	Mazama americana (n = 27)	*Mazama pandora* (n= 30)	*Odocoileus viginianus* (n = 35)
Agriculture (0.09)	**-0.94 Avoided**	0.079 No clear preference	**0.72 Selected**
Secondary growth vegetation (0.04)	-0.064 No clear preference	0.565 No clear preference	0.54 No clear preference
Deforested (0.13) (Agric + SGV)	**-0.83 Avoided**	-0.090 No clear preference	**0.82 Selected**
Tall evergreen forest (0.62)	**0.82 Selected**	-0.22 No clear preference	-0.09 No clear preference
Flooding forest (0.12)	0.50 No clear preference	0.16 No clear preference	-0.32 No clear preference
Short deciduous forest (0.03)	0.51 No clear preference	0.28 No clear preference	0.58 No clear preference

Table 2.4. Habitat use of the three species of deer as rated by Ivlev's index of selectivity for within-buffer habitat composition for deer locations. Selection and avoidance ranks were accepted when the index value was ≥ 0.7 or ≥ -0.70, respectively.

(Figure 2.14, table 2.4); while *Mazama pandora* used habitats in relation with availability, with no clear preferences or avoidances for any particular vegetation type (Figure 2.14, table 2.4). Even when *Mazama pandora* seems to use habitats in relation with availability according with the Ivlev's index of selectivity, the Kruskall-Wallis ANOVA show that there is a highly significant difference in the mean values on the Lowland Flooding forest for this species when compared with the other two species of deer (Table 2.3). This difference in the statistical test and the selectivity indices arises because the later index compares the proportional availability of the Flooding forest with the values obtained for the buffered points. The proportional availability of the Lowland Flooding forest in the study area is comparatively low (21%) in comparison with the more common Tall Evergreen forest (61%). However, these proportions are considerably different for the whole GCR area (36% Lowland Flooding forest and 33% Tall Evergreen forest, see Chapter 4 for details). The results of the Kruskall-Wallis test, therefore might be considered closer to the actual pattern of habitat use by *M. pandora* across the entire GCR with respect to these two habitats (Figure 2.14).

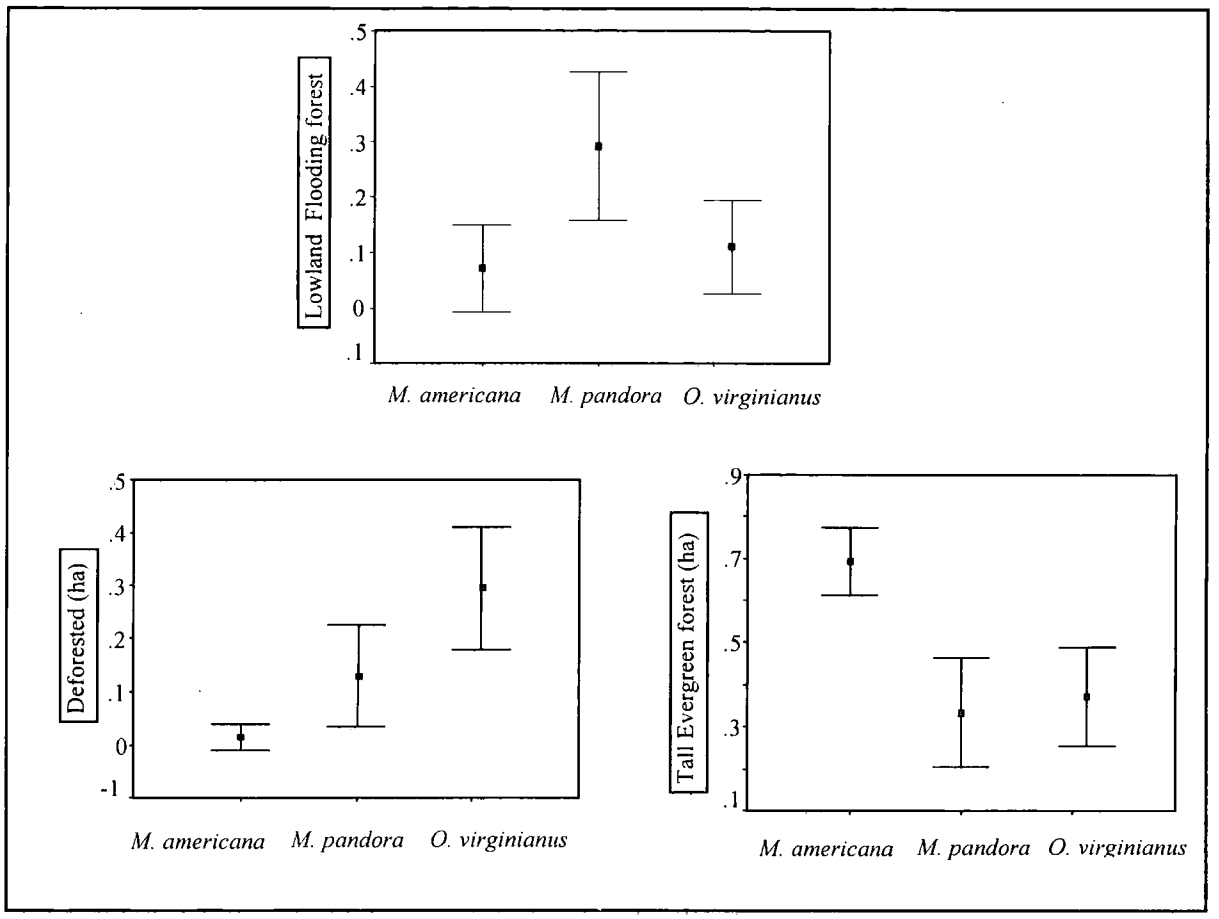

Figure 2.14. Mean and 95% confidence interval of the cover per habitat types of the flooding forest, deforested areas (including agriculture) and tall evergreen forest within-buffered GPS positions recorded for *Odocoileus virginianus* (n = 35 hunting points), *Mazama americana* (n = 27 hunting points) and *Mazama pandora* (n = 30 hunting points).

2.5. Discussion

2.5.1. Population estimations

The results of this study suggest that the two species of *Mazama spp.* are far more abundant in the tropical forest of the GCR than the white-tailed deer. This was evident for both relative abundance and density estimations and for both permanent transects, specifically set for monitoring abundance trends over time and temporary transects designed for detecting changes in space.

Comparisons with other studies are difficult because no other study has ever compared the abundance of this deer assemblage in their whole distributional range. Also, several authors report different indices of abundance obtained with different methods, making comparison even more difficult with other georgraphical areas. However, the relative abundance and density of deer in the GCR is lower than that reported elsewhere in the neotropics (Table 2.6).

The abundance and density of *Mazama* spp. is remarkably similar to that obtained by Wright *et al.* (2000) for Barro Colorado, Panama and by Hurtado-Gonzalez and Bodmer (2004) for Yavari-Miri, Peru (Tables 2.1 and 2.6). Most of the other studies report higher densities for both *Mazama* spp. and the white-tailed deer. The only exception is Naranjo (2003). This author report an even lower density of both species for the Lacandona forest, Chiapas, Mexico. These apparent differences can be the result of real biological dissimilarities in the abundance of these species in different sites or alternatively, might be an artefact resulting from inaccurate sampling designs. For example, several early studies used roads for transect counts (Branan and Marchinton 1987; Bisbal 1994; Wright *et al.*, 2000. Table 2.6). Roads are not random and can be strongly biased by topographic features and therefore habitat types preferred by wildlife that can lead to overestimations (Mandujano and Gallina, 1985; Caughley and Sinclair, 1994). Some recent studies avoided roads and had better transect design but still lack two major assumptions in the design of studies using DISTANCE sampling as the methodological framework: randomisation and stratification of transects (Burham *et al.*, 1980; Buckland *et al.*, 1993; Marquez *et al.* 2001).

Author	Study area	Habitat	Abundance or density estimate ± error measure provided	Transects sampling characteristics Number, type (temporary/permanent), stratification, randomization	Abundance		
					Mazama spp.	*Odocoileus virginianus*	Deer
Bisbal (1994)	Bolivar, Venezuela	Forest, savanna	Deer sightings/10 km walked ± none. "Guesstimates"	Road counts	29		NA
Branan and Marchinton (1987)	Coast of Suriname	Forest, marshes	Deer/km2. "Guesstimates" Track counts ± none Spotlight night counts ± none	Unspecified	1	1-2	NA
Carrillo *et al.* (2000)	Corcovado, Costa Rica	Forest	SER (tracks/100 km) ± s. d.	Permanent transects. Non random. Not stratified. Trails used (roads?)	0.10 ± 0.32	NA	NA
Cullen *et al.* (2000)	Mata Atlantica, Brazil	Forest	Sightings/10 km ± s. d.	Permanent transects. Non random. Not stratified	0.22 ± 0.0.18*	NA	NA
Escamilla *et al* (2000)	Calakmul, Mexico	Forest	Proportions of track vs. sighting counts + none	Permanent transects.	proportions	proportions	
Hurtado-Gonzalez and Bodmer (2003)	Yavari-Miri, Peru	Forest	Density (deer/ km2) + s. e. DISTANCE sampling	Permanent transects. Unspecified details.	1.15 ± 0.51*	NA	NA
Naranjo (2002)	Lacandona, Chiapas Mexico	Forest	SER (tracks/100 km)	Temporary transects. Non random, Non stratified	0.92	0	
		Forest	Density ± s. e. (deer/ km2) DISTANCE sampling	Temporary transects	0.20 ±0.07	0.002*	
Reyna-Hurtado (2002)	Calakmul, Mexico	Forest	SER (tracks/km) ± s. e.	Temporary transects, stratified but not random	8.4 ± 0.033	0.8 ±	
Wright *et al* (2000)	Barro Colorado, Panama	Forest	Density (deer/km2) King estimator *(D = N/(2LR)*	Road counts.	NA	NA	0.93*

Table 2.5. Comparison of estimates of abundance and population density of *Mazama sp* and *Odocoileus virginianus* in previous field studies in Mexico and elsewhere in the Neotropics. * Figures provided here are the mean (calculated for the purposes of this table from original values in the publication) of several areas or habitat types sampled. Compare with table 2.1 for population estimations in this study.

Without random transects, the calculation of deer densities with the program DISTANCE cannot be obtained with reliable confidence intervals (Buckland *et al.*, 1993; Marques *et al.*, 2001; Thomas *et al.*, 2002,). Without stratified transects the effects of site differences (e. g. habitat, hunting intensity) cannot be isolated or controlled and hence cannot be differentiated from each other or from other experimental manipulations (Caughley and Sinclair 1994; Peres 2000). This assumption is of paramount importance, but perhaps because of the difficulty of setting transects in a random, stratified fashion in dense, thick tropical forests, previous research has ignored it almost completely (Table 2.6).

Two-dimensional DISTANCE sampling methods, such as line transects (e. g. Buckland *et al.*, 1993) are more informative than the linear abundance estimates using SER (Carrillo *et al.*, 2000). A major limitation of line transect sampling however is that substantial sample sizes are required. Buckland *et al.* (1993) recommend a minimum of 20 detection events if the distribution of detection distances is unbiased (e.g. random, stratified transects) or 40-80 detection events if the distribution is expected to be biased. Density estimates with this method in tropical forests are therefore strongly limited by the small rate of sightings for many wildlife species (Carrillo *et al.*, 2000; Escamilla *et al.*, 2000; Wright *et al.*, 2000).

The only density estimate that was possible to obtain for both *Mazama* spp. and *Odocoileus virginianus* in this study was by pooling all sightings in all habitat types and all hunting intensity sites into one, so that the total number of sightings (62) can produce a robust density estimate with reliable confidence intervals for both deer groups (*Mazama* spp. and the white-tailed deer). This, however provides only an approximate density estimation and it is impossible to detect any effect of hunting or habitat use preferences on deer density using this method. Only the data obtained from the intensive temporary transect studied during 2001 could be included in this analysis but not for permanent transects monitored from 1996-2001, as the number of deer sightings during the period of monitoring the permanent transects (1996-2001) was even lower. Deer sighting rates were extremely low in this study, particularly for the white-tailed deer (Table 2.1), precluding the use of distance sampling for comparisons of differences of deer densities in time and space. In Chapter 4 an alternative method for visualizing and predicting spatial differences in deer relative abundance using Kernel probabilistic polygons with SER data is proposed.

Unfortunately, the other major wildlife study undertaken within the GCR and hence with the potential to shed light on the accuracy of deer population estimations also has some shortcomings. Escamilla *et al.* (2000) reported proportions of track counts vs. sightings for their relative abundance estimations and these proportions cannot be transformed to actual figures. They used a complicated sampling design with permanent transects in what they call "habitat gradients" (e.g. transects crossing different habitat types) and "conservation gradients" (e.g. transects crossing areas with different hunting intensity). Three transects were set on each site. Roads were used for some transects while others where "cut" throughout the forest. All kind of animal signs were recorded as SER events, even the smell of some species (SanVicente, M. personal communication 2002). It is, therefore, practically impossible to use this study for comparing animal abundance estimates in absolute numbers. Nevertheless, the proportions of deer SER vs. sightings reported in their work is very similar to that found here (approximately 10:1). Once again, the number of sightings of deer in this study was remarkably low (Escamilla *et al.*, 2000)

The only three studies that are directly comparable with regard to relative abundance estimations are those of Carrillo *et al.* (2000), Reyna (2003) and Naranjo (2003). Carrillo *et al.* (2000) estimated 0.1 ± 0.32 *Mazama americana* tracks per kilometer. Reyna (2003) estimated 8.4 SER/km for *Mazama* spp. and 0.8 SER for the white-tailed deer in the GCR. This ten-fold difference between the two brockets and the white-tailed deer, is similar to that found during the present study and to the proportions reported by Escamilla *et al.* (2000). Naranjo (2003) estimated a similar figure for two of the deer species in Chiapas (*Mazama pandora* is absent in the Lacandona forest of Chiapas, Mexico) but "estimated" the density of white-tailed deer using the abundance of *Mazama* spp. tracks (Table 2.5). Whether this is an acceptable density estimate is debatable.
These differences in the abundance of *Mazama* and the white-tailed deer supports the hypothesis that tropical forests are sub-optimal habitats for the highly adaptable white-tailed deer but optimal habitats for *Mazama americana* (Leopold 1956; Eisenberg 1987).

2.5.2. Population sex and age structure

The sex structure of the hunted population of deer (*Mazama pandora*, 34M:23F; *M. americana*, 37M:19F and *O. virginianus*, 11M: 9F) suggests that either hunters are

discriminating for sexes while hunting these species, preferring males over females or, alternatively, that there is an uneven sex ratio in these deer populations. Adult sex ratios of 1:1 and 2:1 are common among the Cervidae (Caughley, 1978; Geist, 1998) and have been documented elsewhere for *Mazama spp.* (Branan and Marchinton, 1987; Bisbal, 1994; Towsend, 1995). Whether these sex ratios truly reflect sex ratios within these deer populations or merely sex ratio differences in hunting success is uncertain. However, sex ratios using the total number of sightings (both on transect and opportunistic observations of deer) are not different from hunting sex ratios (Chapter 4) suggesting that a 2:1 sex ratio is probably the real figure (at least for *M. americana*) in the GCR.

The age structure of the GCR deer population suggests a stable age distribution model with the majority of individuals in the first age categories and fewer individuals in the mature age classes (Caughley, 1978). The finding of two very old individuals (> 12 years old) of *M. pandora* and one >14 years old *M. americana* is within the maximum life expectancy range estimated for the *Odocoilineae* family (Geist, 1998). This finding is also suggestive of a healthy deer population where a few individuals can reach very old ages, but where the majority of the population is within young, reproductive age categories.

Both the life table and the estimation of survival curves are calculations that made broad assumptions. Hunter-gathered data can be biased to certain age classes and no rate of increase is taken into consideration ($r = 0$). To calculate lx it is assumed that all individuals at age 1 survive (therefore $px = 1000$) and that all individuals within the last age class are dead (therefore $px = 0$). These assumptions limit the usefulness of the life table and the survival curves for management purposes because true changes in mortality patterns at species level could not be detected. Much more field data are needed to understand these mortality patterns (Caughley and Sinclair, 1994; Leewenberg and Robinson, 2000). This, however, has not stopped researchers working with subsistence hunters from using them to estimate age structures in deer and other wildlife populations (Towsend, 1995; Bodmer, 1999; Leewenberg and Robinson, 2000; Hurtado-Gonzalez and Bodmer, 2004).

It can be assumed that subsistence hunting samples are less biased than sport or commercial hunting samples, because subsistence hunters normally do not discriminate

among sex and age classes when harvesting deer and other wildlife (e.g. shooting whatever is detected) (Festa-Bianchet *et al.*, 2003; Towsend 1995). However, the sex structure of the deer population in the present study suggest otherwise because the hunters harvested considerably more males than females.

Subsistence hunting related biases in age structure can be less strong than in other harvest scenarios (e.g. sport hunting, culling for population control). Moreover, the use of detailed aging techniques such as that presented here with the combination of both tooth eruption and wear patterns and cementum ring counts for aging deer allows for better accuracy in the determination of harvesting rates per age category at yearly intervals. This, in fact, translates into better accuracy for the determination of survival curves, with less data being lost into large age intervals (e.g. juveniles and adults) (Udevits and Balachey, 1998, Van Deelen *et al.*, 2000). Obtaining substantial numbers of deer skulls and mandibles from hunters can be extremely difficult and time consuming because the deer head is normally consumed by the hunters (Hurtado-Gonzalez and Bodmer, 2004).

According with Hurtado-Gonzalez and Bodmer (2004) the age structures of both *Mazama* species found in the present study are quite similar to that obtained in Peru for *M. americana* and *M. gouasoubira*, suggesting a likely sustainable harvest of the two species. The survival curve of the white-tailed deer is slightly different tending towards a less stable age distribution, but also suggesting a sustainable harvest during the years of study.

These results contrast with the abundance trends obtained for these species during transect surveys where extirpation or near extirpation of the white-tailed deer was documented (Figure 2.6). The small sample size in the skull collection of white-tailed deer could be responsible for this difference and a larger sample size might be able to detect an unstable age distribution pattern. Further studies with the white-tailed deer are needed to clarify this.

2.5.3. Habitat use

There are three levels at which habitat selection can be addressed (1) distribution patterns of animals within the habitat mosaic (i.e., habitat use), (2) the short-term (proximate) reasons for these choices, and (3) the long-term (ultimate) consequences of these decisions. The first level will been examined in the present chapter. Reasons that might

explain the second level will be explored in the next chapter (Chapter 3). Unfortunately the third level cannot be explored as it is argued that a behavioural approach is required to address long term consequences of habitat use decisions.

Ungulates select among habitats depending on certain features such as available cover, forage quality, or presence of roads (McGaffery 1976; Lidicker, 1999,). However, the degree of influence these environmental features impose on habitat selection varies by species and region (Arthur *et al.*, 1996, Tufto *et al.*, 1996).

The habitat use differences detected in this study suggests a relatively clear niche separation between the three species of deer by habitat use preferences. Interestingly, and opposed to what it might had been expected, the Yucatan brown brocket deer seems to be the "true" generalist species (no habitat preferences as suggested by the Ivlev's selectivitry indices for within-buffer habitat composition), and the red brocket deer the specialist species (strong preferences for Tall Evergreen forest supported by both the Ivlev's selectivity and the Kruskall-Wallis ANOVA tests). The white-tailed deer selected agricultural and deforested areas as expected for a deer that is widely recognized as being highly adaptable to habitat changes by human disturbance (Waller and Alverson, 1997) but used all other habitats as expected for availability (as indicated for *Mazama americana* also supported by both the Ivlev's selectivity and the ANOVA tests) . No other study has so far attempted to document habitat use preferences for the Yucatan brown brocket deer, in part because this deer has been just recently recognized as a species (Medellin *et al.* 1998). Most other studies in South America have found both *Mazama americana* and the white-tailed deer as habitat generalists (Etzenhouser *et al.*, 1998, Branan and Marchinton, 1987; Yanosky and Mercolli, 1994; Bodmer, 1999). However, the fact that non-parametric statistics had to be used together with the small sample sizes in GPS positions suggests that very little power for strong statistical differences exists. Therefore, these patterns in habitat use should be taken as preliminary results and further studies are necessary.

The high habitat heterogeneity of the Greater Calakmul and Peten regions in the southern Yucatan Peninsula provides a unique mosaic of vegetation types found nowhere else in Mesoamerica (Martinez and Galindo-Leal, 2003). More than 28 major vegetation associations had been recognized based on the structure , composition and plant

dominance within the GCR. This high habitat heterogeneity may partially explain for the deer habitat use patterns documented here. *Mazama americana* might have been evolved as a habitat specialist of the more common tall evergreen forest to avoid competition with the other two deer species. Whilst *M. pandora* is an endemic species of the Yucatan (and possibly Peten regions in Guatemala and Belize) (Medellin *et al.*, 1998; Weber and Gonzalez 2003) it can also utilise a much more diverse group of habitat/vegetation types than *M. americana* (Medellin *et al.*, 1998). While this might contradict in part what it is usually expected for an endemic species (e. g. endemics tend to be habitat specialists) (Arita *et al.*, 1999) this particular endemic species has to be seen within the context of the whole biogeographical characteristics of the southern Yucatan Peninsula. This region is considered by many ecologists as an "island" within the continent (Miranda 1958; Pennington and Sarukhan,1998; Schulze and Whitacre, 1999) with unique topographic and vegetation characteristics.

The origin of the *Cervidae* is still somewhat obscure, however it is now apparent that the adaptive radiation of true deer probably began in Eurasia. The small genera of *Pudu* and *Mazama* are probably secondarily small, deriving from an ancestral form that was larger (Eisenberg, 1987). The close philogenetic relationships of the *Odocoileus* and *Mazama* species has been proved by finding both genera in the same mitochondrial DNA cluster (Cronin, 2003) and with very similar allozyme allele frequencies (Smith *et al.*, 1986). While much is still speculative, it is known with some certainty that deer entered South America in the late Pliocene (Eisenberg, 1987). However, the exact origin of the adaptive radiation of both *Odocoileus* and *Mazama* species is still unknown. The creation of "insular-like" habitats during periods of glacial *maxima* derived from the vastly reduced rainfall over many parts of South America has generated testable hypothesis concerning adaptive radiation in butterflies, birds and mammals (Muller, 1973). Perhaps, the dwarf races of *Mazama* evolved during such habitat fragmentation period (Hershkovits, 1982). It is hypothesized here, that *M. pandora* possibly evolved as a habitat "specialist" for this unique mosaic within its distributional range in theYucatan Peninsula (making of it an endemic species by definition), but as a habitat "generalist" at a more regional scale within a specific region of its distributional range.

These differences in habitat use preferences have potential implications for the conservation and management of the three species of deer. The species that are not

habitat specialists (*M. pandora* and *O. virginianus*) and that can easily disperse over the unsuitable habitats, might not be severely affected by changes on the forest cover. In contrast, deforestation of the dominant but more sensitive Tall Evergreen forest can severely affect the dispersal capabilities of *M. americana* as a habitat specialist of this vegetation type. This can eventually lead this deer into competition with the other two species. If we assume that the relative abundance of the two brockets is similar, then a change in habitat composition favouring the brown brocket and the white-tailed deer, would set the red brocket deer at a numerical disadvantage for potential competitive interactions.

Maintaining a habitat mosaic where the Tall Evergreen tropical forest is dominant will likely favour the coexistence of these three species of deer. Changing it, through slash and burn agriculture and other causes of deforestation might result in a competitive advantage for the two generalist species. If this occurs in conjunction with over-harvesting by subsistence hunters, a scenario may result where populations of the red brocket deer could be locally extirpated.

CHAPTER THREE

Diet and habitat ecology of three sympatric deer in a tropical forest

3.1. Introduction

3.1.1. Diet selection studies

An understanding of diet selection is fundamental to exploring interactions between wildlife and their habitats (Hanley, 1997). The process of diet selection determines both the quality and the quantity of food intake and hence, the nutritional status of individual animals, their time and activity budgets, their physiological condition, growth rates and potential reproductive and survival rates (Caughley and Sinclair, 1994). In the case of primary consumers, it also determines which plants are consumed, where, when and how much. Diet selection therefore plays a central role in herbivore-plant interactions, with direct consequences to the structure, species composition and ecological relationships of plant communities and their ecosystems (Bleich *et al*; 1997; Hanley, 1997; Waller and Alverson, 1997). Indeed, diet selection studies formed a central part of the wildlife management discipline for many years. The evolution from merely descriptive studies, for example, plant preferences, to more dynamic models involving landscape habitat analysis in the diet selection process, closely match the evolution of the wildlife science as a whole.

Diet overlap is of interest for wildlife managers because it allows the assessment of interactions between wildlife species, livestock and their habitat. Dietary overlap studies are site-specific and are related to the quality of certain habitats (Hansen and Reid, 1975). In fact, the degree of dietary overlap is central for determining potential competitive interactions in sympatric species (Caughley and Sinclair, 1994; Krebs 1994). Dietary overlap between different related herbivore species is indicated by common preference for specific plants and plant parts. Therefore, common preference may be detected at certain levels of the plant community (Hansen and Reid 1975).

Ungulates display variable degrees of preference in certain terrain and plant communities and for particular plant species and plant parts. Ungulates select among habitats depending on certain features such as available cover, forage quality, or presence of roads (Hanley, 1997). However, the degree of influence these

environmental features impose on habitat selection varies by species and region (Clutton-Brock *et al.*, 1982).

Early studies of diet selection by deer were entirely descriptive. Studies of wild deer diet usually by rumen analysis and later by fecal analysis, led to an extensive empirical literature on food habits of deer (Branan *et al.*, 1985; Stallings 1986; Bodmer, 1989). With this studies, it became evident that tremendous variation exist in diet composition of deer diets and more elaborate models begin to emerge (Hanley 1997).

While a large amount of information exists in the literature about dietary selection by deer, diet overlap, nutritional requirements and its relationships with habitat in temperate environments, the information available for tropical environments is much more scarce.

A handful of studies have attempted to determine the diet of forest-dwelling deer in Neotropical environments. Even less work has been done on finding the relationships of deer diet with habitat characteristics in tropical forests. Branan *et al.* (1985) were pioneers in determining the diet of the deer assemblage (composed of three deer species) in Suriname forests, but failed to link deer with habitat characteristics because their rumen samples came from separate regions and habitat types within the country. Stallings (1985) studied the diet of *Mazama gouasoubira* in the Boreal Chaco of Paraguay, but his study is purely descriptive of plant species and parts selected. More recently Bodmer (1989, 1991) studied the diet of *Mazama americana* and *M. gouasoubira* in Peru with the goal of understanding the intricate plant-herbivore relationships at the ungulate community level in the Amazonian forest. Finally, a recent study described the diets of this same two *Mazama sp.* in the French Guyana, but once again the authors disregarded the habitat characteristics where the samples of deer stomach contents came from (Gayot *et al,*. 2004).

3.1.2. Diet-habitat relationships

To understand diet-habitat characteristics in deer it is often necessary to follow a spatial and temporal approach where both diet and habitat ecology parameters are measured, ideally in a simultaneous fashion. For this, information on the exact location where

animals perform their foraging activities and the timing of this ought to be recorded. This is extremely difficult in tropical environments, because the climate and environmental conditions does not favour a behavioural approach to tackle this problems (but see also "Technical difficulties for the study of tropical deer populations" in Chapter 1) . Therefore, a different approach is necessary if information on the diet as it is related with habitat ecology is ever going to be obtained.

The advancement on GIS/GPS technologies opens-up a new possibility for diet-habitat wildlife studies in neotropical forests. The same approaches followed in the past for deer diet determination (e.g. collection of stomach samples, micro-analysis of faeces contents) and plant-herbivore interactions, can now be linked with habitat characteristics by recording the exact coordinate positions where the samples are being taken and linking them to GIS-based habitat maps (Ormsby and Luneta, 1987, Beutel *et al*; 1999).

Moreover, to understand diet-habitat interactions in deer it is necessary to obtain information on food availability. Food availability for primary consumers is determined by the phenological patterns of plants from which animals depend on (VanSchaik *et al.*, 1993). While information on the phenology of tropical forests is widely available in the literature, tremendous variation exist in different tropical forest sites, because phenology is regulated by the endogenous cycles of plant physiology and has both proximate and ultimate factors determining its occurrence (Bullock and Solis-Magallanes, 1990; Borchert, 1994, 1999; Newstrom *et al.*, 1994VanSchaik *et al.*,1993, Borchert *et al.*, 2002). Temporal patterns of flowering and fruiting of species in tropical rainforests are usually interpreted as: (i) endogenous rhythms indirectly affected by environmental factors through physiological mechanisms of individual plants, (ii) environmental "triggers"; such as storm rains, changing intensities or periodicities of light (proximate factor) (iii) selective pressures exerted by animals acting as pollinators, dispersers and predators (ultimate factor) (Borchert, 1999; Reich, 1995).

Therefore, the study of phenology of plants as in indicator of food availability for primary consumers must follow local (or at least regional) approaches, since local variations in both proximate and ultimate factors are likely to occur and extrapolations

from different sites are not only of little utility but can be misleading if management decisions are to be made with this information (Borchert, 1994; Reich, 1995; Kudo and Suzuki, 2002). If the phenological characteristics of groups of highly preferred plants used by wildlife can be determined, indices of food availability can usually be obtained from this information and diet-habitat links can now be established.

Diet and phenology studies in the tropics have lead to the identification of Keystone Plant Resources (thereafter, KPR). KPR can be defined as fruits, seeds, floral, nectar and bark produced by a small set of species in a local flora which serve a disproportionately large trophic importance to a loosely defined group of consumers (Terborgh, 1986; Mills *et al.*, 1993). Following this definition, Peres (1999) proposed four criteria for the identification of KPR in tropical forests: (1) Temporal redundancy (TR). Defined as the degree to which the availability of a potential KPR synchronizes with that of the combined pool of alternative food resources used by a consumer assemblage. In this terms, a resource may range from entirely indispensable (low TR) if it becomes available during periods of maximum overall fruit scarcity, to completely substitutable (high TR) if it becomes available only during months of peak availability of alternative plant resources consumed; (2) Consumer specificity (CS). Is an inverse function of the percentage of frugivorous species in a local vertebrate assemblage reported to exploit the putative KPR; (3) Resource reliability (RR). Defined in terms of the degree to which a potential KPR at a given site will predictably become available every year to sustain consumers, and in the case of low redundancy resources, through annual periods of scarcity, and; (4) Resource abundance (RA). Conceptualised in terms of the crude abundance of a potential KPR at a given site, on the basis of a given patch density of a given resource and, when available, some indication of patch size.

The identification of KPR for certain components of the vertebrate community with high ecological and economical importance might be vital to the incipient attempts to manage deer populations in the GCR and elsewhere in Latin America.

3.2. Chapter aims.

In this chapter, I will present the results of a study aimed to determined the diet of deer and its relationships with habitat ecology parameters, such as forest types, plant fruit phenology and food availability for an assemblage of three sympatric deer species; the Red brocket deer (*Mazama americana*), the Yucatan Peninsula Brown Brocket deer (*Mazama pandora*) and the white-tailed deer (*Odocoileus virginianus*) in the Greater Calakmul Region (GCR), southern Yucatan Peninsula, Campeche, Mexico.

Investigating the diet of the three species of deer was a major objective of this study with the ultimate goal of linking the diet of deer with the habitat ecology parameters mentioned. Exploring the role of each species of deer as frugivores, browsers and seed predators and the ecological niche of each species at the trophic level as primary consumers was a secondary goal.

The emphasis in phenology was to reveal broad, community-wide fruiting patterns of the main plant species forming the core of the diet of deer in the GCR. With this, food availability (thinking of fruits as one of the major components of deer diet in tropical forests) could be assessed. The determination of likely candidates as "keystone plant resources" (hereafter, KPR) for deer was a secondary goal in the phenology study and it is widely discussed. In particular, the "Non-redundancy" concept in determining keystone plant resources (Peres, 1999) is examined as criteria for the inclusion (or exclusion) into the KPR categorization of two of the most important plants forming the diet of deer in the GCR.

The results obtained are dissected against other deer diet-habitat studies in both tropical and temperate forests and analysed within the framework of the habitat selection theory by resource availability as the proximate factor (Clutton-Brock *et al,*. 1982). Finally, the relationships of diet, plant phenology and food availability (as rated by fruit phenological patterns) and deer abundance were examined. To the best of my knowledge, this is the first study of its kind for an assemblage of three sympatric species of tropical forest-dwelling deer north of the Amazon.

3.3. Methods

3.3.1. Diet.

3.3.1.1. Feeding habits.

Stomach contents of the three species of deer were collected systematically over a period of three years (1997-99) and opportunistically from 2001-2002. Those hunters willing to participate in the study were provided with large Zip-Lock bags, jars and 10% formalin that they took with them on their hunting expeditions. Hunters were trained in the collection and preparation of the samples and were also provided with a diary where they recorded relevant information (deer species, common name, location, etc.). The exact location of the deer kill was later pinpointed using map coordinates and a GPS hand held receiver (see Chapter 4 for details on the GPS techniques used).

The samples were later washed through a fine 0.5 mm^2 mesh screen, dried and analysed following Bodmer's (1989) technique by comparing representative examples of seeds, fruits, flowers, leaves and stems against voucher material at the National Herbarium in Mexico City. An expert botanist (Mr. Esteban Martinez. Senior Field Taxonomist, National Herbarium, MEXU, Mexico City.) with more than 10 years experience in the taxonomic identification of plant material in the area, helped in the identification process. A collection of representative samples from each plant species (mainly seeds and fruits) where deposited at the National Herbarium, UNAM, Mexico City. Both aggregate percent volume (APV) and frequency of occurrence of each plant item were calculated for each stomach content and used as standard units of occurrence. Plant nomenclature follows Martinez *et al.* (2001) and Martinez and Galindo-Leal (2003).

A thorough identification of plant material was hampered in some of the samples (n = 19, from a total of 52 stomach samples) collected by hunters as these were actually sub-samples of stomach contents taken. This occurred because of the large size of some stomach samples (especially those of white-tailed deer kills) and the hunter either was unwilling to carry the whole sample back home or he simply forgot to carry enough bags or jars to carry them back to the community. Some of these sub-samples were later identified as coming from rumen or reticulum based on tiny pieces of mucosa present in the contents, by interviewing the hunter about anatomical aspects of the place were the sample was taken, particle size of plant material in the sample and therefore given the

amount of digestion that had taken place, and/or a combination of the above. Samples and sub-samples were compared to determine the amount of unidentified plant material in order to obtain correction factors for the calculation of APV volumes.

Log-likelihood G tests (Zar 1996) were used to look at differences in the diet of the three species of deer in relation with season and plant part consumed. Observed and expected values were calculated using the accumulated proportions of items in the diet (e.g. fruits, leaves, stems) for the paired comparisons between deer species. Therefore, both observed and expected values are true observational measurements.

3.3.1.2. Diet overlap

Johnson's rank index of preferences (Johnson, 1980a, 1980b, Krebs 1989) were used to look at preferences in the selection of plants at the family, genus and species level for the three species of deer. The Johnson's index (Johnson 1980a) provides estimates of preferences of plants for the three species of deer. The smallest the value of the rank preference index, the most preferred the resource is (Krebs 1999). The Johnson index is a non-parametric method that makes use of the ranks of usage and availability to carry out a multivariate test where the variables are habitat or food types. It is a difficult method to implement without suitable software since it involves the inversion of a matrix. However, there is a public domain program (PREFER) available that does the necessary calculations (Johnson, 1980b).

Diet overlap between the three species of deer was estimated with the Standardized Hurlbert's Niche Breadth Index (thereafter, Hurlbert's index) (Krebs, 1989). Hurlbert's index extends the information given by Levin's measure of diversity to include the effects of proportional availability of each resource. Levin's diversity measure is a rectilinear measure of preferences that disregards availability (Krebs, 1989).
Both indices indicate a lack of trophic segregation based on the frequency of occurrence of each plant item among the diet of the three species of deer (Krebs, 1989). Levin's measure of diversity is calculated as:

$$B = (\Sigma p_i^2)^{-1} \qquad \text{(Equation 1)}$$

where p_i is the proportional use of a food item relative to other food items. B ranges from 1 to n (n = total number of food item categories; fruits, seeds, leaves.).
Hulbert's standardised niche overlap index transform Levin's measure with the following formula:

$$B_s = (B-1)/(n-1) \qquad \text{(Equation 2)}$$

where B = Levins' measure of diversity and n = number of food categories.

The taxonomic family of plants were used as food categories to calculate both Johnson's and Hurlbert's indices. The family was chosen to broaden the spectrum of food preferences and diet overlap into wider taxonomical ranks that might bring more biologically meaningful, community-wide patterns than the genus or species levels. The cumulative APV of all plant parts (e.g. leaves, fruits, etc) was calculated at the family level and used as food categories for the calculation of both indices.

The software program PREFER (version 1.2 for Windows downloaded from http://www.npwrc.usgs.gov/resource/tools/software/ on April 2003) was used to obtain Johnson's index and the program KREBS for Windows (Krebs, 1996) was used to calculate the Hurlberts's (and by default Levin's measure of diversity) indices. The program PREFER performs calculations described in Johnson (1980a) to determine the preference of *J* individuals for *I* components (for example, habitat types or kinds of foods) using availability and use data. The method is based on ranks of the components by availability and by use. Accordingly, a virtue of the method is that it provides comparable results whether a questionable component is included or excluded from consideration. Other methods of determining resource preference depend critically on the array of components that the researcher deems available to the animal; such decisions are often arbitrary. PREFER tests the hypothesis that all components are equally preferred and compares components using a multiple comparison procedure (Johnson, 1980b).

3.3.2. Habitat ecology

3.3.2.1. Vegetation mapping for deer habitat types

A number of land cover/land use projects had been developed in the GCR in recent years. These projects involved the mapping of vegetation, land cover and land use characteristics of the GCR with the use of satellite images, low altitude aerial photographs and ground verification (Martinez and Galindo-Leal 2003, Garcia-Gil *et al.*, 2000, Turner *et al.*, 2001). To map deer habitat types and vegetation classes in the study area, extensive use of two major existing vegetation mapping data sources of the GCR was made (Martinez and Galindo-Leal, 2003, Turner *et al.*,2001). The ArcView and Idrisi coverages of the GCR were obtained and used with permission by the authors from Stanford University, California (Galindo-Leal, C.) and Clark University, Massachusetts, USA (Turner, B. J.), respectively. Martinez and Galindo-Leal (2002) provide a very detailed vegetation classification of the GCR split into 28 vegetation classes, while Turner *et al.*, (2000) classification is composed of 9 land cover/land use classes that covers a larger area in the southern Yucatan Peninsula.

These two sets of GIS layers were obtained with similar methods using maximum likelihood supervised classifications that included bands 2, 3, 4, 5 and 7 of a series of LANDSAT Thematic Mapper Images of the GCR from 1995 and 1996 (Weiss *et al.* 2000; Martinez and Galindo-Leal, 2003) and 1996-1997 (Turner *et al.*, 2001). Both coverages provide a 30 x 30 meters pixel resolution, but some differences exist in the way the authors validated their respective data sets.

Martinez and Galindo-Leal (2003) used a predictive model based in a CANOCO (Canonical Correspondence Analysis) that incorporates expert botanical knowledge on dominant tree species and environmental and topographic variables validated with 620 descriptive sites/training points for the satellite images of the GCR from 1995 and 1996 to produce a detailed coverage of vegetation associations (Weiss *et al.*, 2000; Martinez and Galindo-Leal, 2003).

Turner *et al.*, (2001) used a PCA (Principal Component Analysis) approach for "ground-truthed" data obtained in their 7 vegetation classes within a frame of continued verification and validation with training site points of the 1996 and 1997 satellite

images of the GCR (and other areas of the southern Yucatan Peninsula). Moreover, Turner *et al.* (2000) cross-validated their satellite image based coverages with high-resolution aerial photographs taken at low altitude during the same study period. However, neither of these classifications adjusted to present needs to mapping deer habitat classification, either because they were too detailed at the level of vegetation associations (Martinez and Galindo-Leal, 2003) or because included vegetation associations irrelevant for the purpose of the present study (e. g. invading fern fields) (Turner *et al.*, 2000). Therefore, the maps were modified accordingly.

For the modification of these coverages, 640 training points using a Trimble II Geoexplorer GPS hand-held receiver (Trimble Inc., Palo Alto, California) were collected in the five vegetation associations considered as major habitat types for deer. The training points were located in typical deer habitat (where deer signs or presence was previously detected) and the vegetation type was assigned with the advice of an experienced botanist and first author of the main coverage used here (Esteban Martinez, National Herbarium of Mexico, UNAM, Mexico).

The new vegetation classes were those considered relevant to deer habitats such as Tall Evergreen forest, Lowland Flooding forest, Short Deciduous forest, Second Growth vegetation and Agricultural areas. A sixth vegetation class was incorporated as "Deforested" by pooling both Agricultural and Second Growth vegetation areas.

Finally, the original classifications of vegetation associations were reduced to these six "deer habitat" classes. Martinez and Galindo-Leal (2003) classification is based on a forest type (e.g. Tall evergreen forest) classification subdivided in vegetation associations (e. g. Ramon Forest, Chicle forest, etc.) according with the dominance of major trees and plant species composition. The reduction to the new six class system was straightforward, since all vegetation associations might be assimilated into the new classes without losing many important coverage information into "no data" pixels.

The new vegetation classification focuses on the main vegetation associations related with the data base of deer habitat use, deer diet and tree phenology of the main tree species found in the diet of deer.

The ArcView coverage of Martinez and Galindo-Leal (2003) was used as the primary vegetation map. However, the accuracy of the new classification was cross-examined with the Idrisi coverage (Turner *et al.,* 2000). Percentages of accuracy were then calculated for the 640 training points (corresponding to 128 per class) for each new classification class and for both coverages. For this, each GPS training point was considered as "accurate" when the original field-assigned vegetation class was the same as that corresponding with the new coverage classification. Low accuracy values were expected with this tight validation criteria, given the variability of GPS reception in different forest types, the band signal overlap among satellite signals for similar vegetation classes and other factors. However, given that the six vegetation classes chosen as major deer habitat types were quite different from each other, a decision to stick with this criteria was made.

The classification system was accepted for each vegetation class when the accuracy of corresponding training points was >80%. The only exception was the Short Deciduous forest for which even lower accuracies were predicted based on overlapping band signals with other vegetation classes such as Second Growth vegetation. This forest type was considered of minor importance, though, because it represents less than 2% of the forest cover in the study area (Nuevo Becal land-holding).

Additionally, a complete set of extra GIS coverages, including roads (motor-ways, dust roads and logging roads, water-holes, land tenure (limiting community land boundaries), land use (agriculture) and the delimiting polygon of the Calakmul Biosphere Reserve (protected area limits from private and community lands) was obtained for the study area. These are ArcView (ESRI, Redlands, California) based coverages created from digitalized, high-resolution colour aerial photographs taken at low altitude from 1998-1999 (Garcia-Gil *et al.,* 2000). A few roads and logging trails within the study area that were missing from the original road coverage and were considered important for the analysis of deer habitat or hunting information were later digitalized using GPS position of the roads and the sometimes obvious location and direction within the vegetation land use/land cover coverages. ArcView 3.2, Idrisi 32 (Clark Labs. Clark University, Boston, MA) and ArcGIS 2.1 (ESRI, Redlands, CA)

were used as the GIS platforms for coverage analysis, verification of training points and creation of the new vegetation classification.

3.3.2.2. Forest structure and composition

To look at forest structure and composition in different habitat types, the Canfield line intercept technique (Brower *et al.*, 1990) was used. This is a standard forestry technique to assess forest stands that uses lines (transects) of 100 meters-long (or the first 100 trees sampled, whatever happened first) to measure a number of tree parameters. The lines were located at the beginning of the middle kilometre of three of the permanent transects cut for monitoring deer abundance (see Chapter 2). Three transects were chosen on each forest type laying on typical undisturbed deer habitat over the three major habitat forest types (Tall evergreen forest, Short deciduous forest and Lowland flooding forest). Therefore two replicates were made for each forest type (e.g. one Canfield line per habitat type per transect).

With the help of a trained biologist and a botanist, the following information was collected on each Canfield line per forest type (data for trees larger than 30 cm of DBH (diameter at breast height): Species, tree height, DBH , distance to the nearest neighbour (of the same diameter criteria) and canopy cover. I first trained myself in tree height measurement using an electronic range-finder and when my measurement assessments where accurate enough (approximately 90% accuracy), I began estimating tree eight by sight, validating height estimates against other colleagues using the rangefinder. Canopy cover was estimated as closed (zero value) or open (one value) using a "moose-eye" tree canopy densitometer (Forestry Suppliers Inc, Mississipi, USA) and the reading was taken at one arm length from the tree trunk (Condit *et al.*, 2000). Transects were located at random, using the GPS location of the larger deer abundance transect (again see Figure 2.1, Chapter 2) and random numbers in each habitat type to locate the Canfield lines' 100 meters sub-transect. Analysis of forest structure and composition were performed with simple diversity measures (species richness, Shannon-Wiener diversity index) (Krebs 1989) and one way analysis of variance (ANOVA) for log-transformed data (Conover, 1980; Zar 1996)

3.3.2.3. Fruiting phenology of major plant species on deer diet

From January 2001 to March 2002, the fruiting phenology of some of the major plant species found in the analysis of deer stomach samples was studied. For this, I followed the standardized methodology outlined by Van Schaik *et al.* (1993) and Newstrom *et al.* (1994). Three sampling plots (squares of approximately 2 hectares in size) were set in the three major forest habitat types used by deer (Tall Evergreen forest, Short Deciduous forest and Mixed Lowland flooding forest). In each plot, ten specimens of the dominant plant species in the diet (APV in diet) were marked (with paint and aluminium tags). The species monitored in the Tall Evergreen forest (n = 240 trees) were eight: Zapote tree (*Manilkara zapota*), Ramon (*Brosimun alicastrum*), Laurelillo (*Nectandra salicifolia*), Lecherillo (*Thevetia gaumeri*), Mamba (*Pseudolmedia spuria*), Guayabillo (*Eugenia sp.*) and two palm species: the Xiat palm (*Chamaedora ernesti-augusti*) and the Guano Palm (*Sabal mauritiformis*). In the Short Deciduous forest, six species were chosen (n = 180 trees); Zapote (*Manilkara zapota*), Ramon (*Brosimun alicastrum*), Laurelillo (*Nectandra salicifolia*), Lecherillo (*Thevetia gaumeri*), Guayabillo (*Eugenia* sp.) and Majahua (*Hampea trilobata*). In the Lowland Flooding forest, six species were studied (n = 180 trees) as follows; Zapote (*Manilkara zapota*), Guayabillo (*Eugenia* sp.), Majahua (*Hampea trilobata*), Palo Tinto (*Hematoxilum campechianum*), Tripa de cochino (*Hyperbaena winzerlingii*) and Che-chen (*Metopium brownei*).

Mature and apparently healthy trees of no less than 35 cm. DBH were chosen for the emergent tree species (Zapote, Ramon, Majahua, Palo Tinto and Che-chen) and apparently healthy individuals of no less than 20 cm. DBH where selected for the non-emergent understory species (Laurelillo, Mamba, Lecherillo, Tripa de Cochino and Guano Palm). Two exceptions from these selection rules were the Xiat palm (*Chamaedora ernesti-augusti*) and the Guayabillo tree (*Eugenia* spp.) because they are short, low-DBH-at-reproduction species (Pennington and Sarukan, 1998). For the abundant Xiat palm, mature and healthy individuals were selected at random and tagged with flagging tape. Selection of Guayabillo trees was more difficult because they are indeed a complex of seven or more similar species that are extremely difficult to distinguish in the field and likely with very different life histories (Martinez, E. personal

communication, 2000). Therefore, the criteria for selecting Guayabillo trees was the presence of reproductive material (fruits or flower buds at the time of setting the plots.) most commonly used by plant taxonomists to differentiate among complexes of similar species. Most Guayabillo trees were from 2.5 to 5 cm. DBH and usually less than 3 meters tall.

Species abundance and dominance was used as criteria to choose plants sampled in each habitat type. Dominant species in the diet of deer that occurred in all habitat types were usually sampled, but this was not always possible. For example, the Ramon tree (*Brosimum alicastrum*) although dominant in the diet of the tree species of deer, does not occur, or it is extremely rare, in the Lowland Flooding forest. The two most common plant components in the deer diet; the fruits of the trees *Manilkara sapota* and *Brosimum alicastrum* were included in the two habitat types were they commonly occur (Tall Evergreen and Deciduous forests) in order to make comparisons on abundance, fruiting phenology, seed rain and to test for differences in availability as the major components on the diet of the three species of deer. These two species were chosen, because together they represented from 30 to up to 50% of the APV of the majority of the deer stomach contents. Therefore, these two species form the core of the deer diet and were considered as potential candidates as "keystone plant resources" for deer in the study area (Van Schaik *et al.*, 1993, Peres, 1999).

The location of the phenology plots (but see also figure 1.1 in Chapter 1) was a major decision because easy access was needed for the intensive sampling effort required and at the same time representative, undisturbed (e.g. no logging activities) examples of each vegetation class was needed. A trade-off between this two characteristics existed, because easily accessible forests are usually subject to forest disturbance in the GCR and the likelihood of disturbance (logging) in a one-year period of continuous monitoring was high. The plots were then located with the help of the GIS and road maps as well as from interviews with community forestry authorities to minimize the effect of disturbance and permit easy access to the plots.

A total of 600 marked trees were visited and monitored once every month for readings in the following parameters: fruit status (mature, immature), fruit cover availability on

the tree (FCT) measured in a 0 to 4 scale, fruit availability on the ground (seed rain) measured in a 0 to 4 scale, and presence-absence of leaves and flowers (Van Schaik *et al.*, 1993). The 0 to 4 scales are, of course, equivalents to 0, 25, 50, 75 and 100% values. Some environmental characteristics (such as rain, flooding status, disturbance by humans) were also noted on each visit in an attempt to obtain correlations with fruit production and availability.

To analyse fruit phenology data, differences in phenology time and fruit production were analysed first graphically with both time series frequency charts and "rose diagrams" (or circular histograms) (Zar 1996). The running mean values of FCT and seed rain were calculated per habitat type and then pooled to obtain a general fruit phenology pattern for the study area. Phenology was not thoroughly analysed statistically (other than the determination of fruiting percentages, running mean values and Kruskall-wallis tests for this mean running values between habitat types) for three reasons: (1) The main goal of the study was the determination of broad, community-wide patterns of fruiting phenology as indices of food availability for deer, (2) the rank values proposed by Van Schaik *et al.* (1993) are practical for determining broad community-wide patterns but the ranking system does not left much room for detailed quantitative analysis, and (3) the sampling period was short (11 months) precluding the use of circular statistics (Zar, 1996) and therefore the effects of seasonality cannot be analysed quantitatively.

3.3.2.4. Fruit production and availability

3.3.2.4.1. Seed rain

Patterns of fruit availability on the ground (hereafter called "seed rain") were estimated by recording the approximate amount of fruit available on the ground in a radius equivalent to the same area covered by the spread of the tree canopy cover (same scales as phenology measurements). Seed rain was defined, for the purposes of the present study, as the ratio of fruits observed over the ground against the amount of fruit present on the tree (FCT). The seed rain was considered as a measure of fruit density and therefore potential availability for deer and as a gross fruit biomass indicator when a large amount of fruits where evident in the forest ground. A "seed rain index" was obtained by calculating the ratio of fruit production (percentage of fruit upon the tree,

FCT) and the amount of fruit in the forest ground immediately adjacent to the same tree under surveillance, expressed as a ratio. These ratios were also calculated for the percentage of trees that actually presented fruits. Differences in timing of fruit phenology and seed rain peaks where represented graphically on rose diagrams using the ratios as percentages (Zar 1996).

3.3.2.4.2. Seed predation and dispersal.

To investigate the possible role of deer in seed predation and dispersal, 730 fresh deer pellet groups were collected (opportunistically) during field outings from January 2001 to March 2002. Some hunters also collaborated by collecting fresh pellets for the study. It was impossible to distinguish between pellets from *Mazama americana* and *M .pandora*, because the size and shape of pellets are broadly equivalent in these species, therefore all pellets from these two species were pooled into *Mazama sp.* Deer pellets were assigned as being from the white-tailed deer (based on the much larger size, rounder shape and association with white-tailed deer tracks). The bags containing the pellets were labelled and sun-dried in trays for a period of two weeks. Later, all pellets were dissected, subsamples were carefully hand-ground in a mortar and all identifiable remains of seeds and fruits were collected. These remains were later compared with the previously classified collection of seeds obtained from stomach samples and with herbarium specimens deposited at the National Herbarium in Mexico City. The goal was to obtain and identify all seed remains as evidence of seed predation and to collect complete seeds for germination experiments back in the laboratory (Bodmer, 1991; Vazquez-Yanes and Orosco-Segovia, 1993; Fragoso, 1997). Eighteen pilot germination experiments of retrieved seeds were performed *in situ* in local soil with permanent shade and sporadic watering (in an effort to mimic natural soil humidity patterns) to look at the viability of seeds collected from stomachs compared to those collected from faeces (six experiments for each deer species, three with stomach material and three with faeces material). Most seed remains were in a poor anatomical state and these pilot trials were needed to weight the value of further laboratory work. Unfortunately, a fungus infestation in the field of all the dissected deer pellet material (due to high relative humidity conditions in the Zoh-Laguna village during the rain season of 2001 and a failure in the storage device and procedures) precluded any further work with this material.

3.3.2.4.3. Seasonal and temporal relationships of deer abundance, diet and fruiting phenology.

The seasonal and temporal relationships of the abundance of deer (as rated by sign encounter rate (SER/km) see also Chapter 2), deer diet (as represented by fruit consumption) and temporal and spatial fruiting phenology patterns were investigated. For this, the running mean values of these three parameters were calculated and graphed. The running mean value of the SER index of abundance of deer was obtained from the monthly monitoring of deer signs from 1996 to 1999 in three permanent transects (see Chapter 3 for details). These seasonal and temporal patterns of both fruit availability and consumption (accumulated APV values in diet per month) are also presented in the form of "rose diagrams" (Zar, 1996) that were considered as a better graphical representation for this associations. The links between monthly timing periods between events can then evaluated.

3.4. Results

3.4.1. Deer diet

3.4.1.1. Feeding habits and diet overlap

In total, 52 stomach samples of the three species of deer (18 *Mazama americana*, 17 *Mazama pandora*, and 17 *O. virginianus*) were collected with the help of cooperating subsistence hunters.

There were major differences in the diet of the three species of deer. *Mazama americana* consumed mostly fruits with its diet comprising up to 80% of fruits and seeds year-round. In contrast, *Mazama pandora* showed strong seasonal variations in its diet, being mainly a frugivore during the dry season (63% fruits) and largely a browser during the wet season (with 60 % of the diet being comprised by leaves and stems). The white-tailed deer diet was closer to that of a browser year-round with up to 70% of its diet being comprised by leaves and stems year-round, although it also showed some seasonal variations and more fruit consumption during the wet season. The consumption of flowers by the three species of deer was minimal and occurred only during the wet season by both *Mazama* species and during the dry season by the white-tailed deer (Figure 3.1).

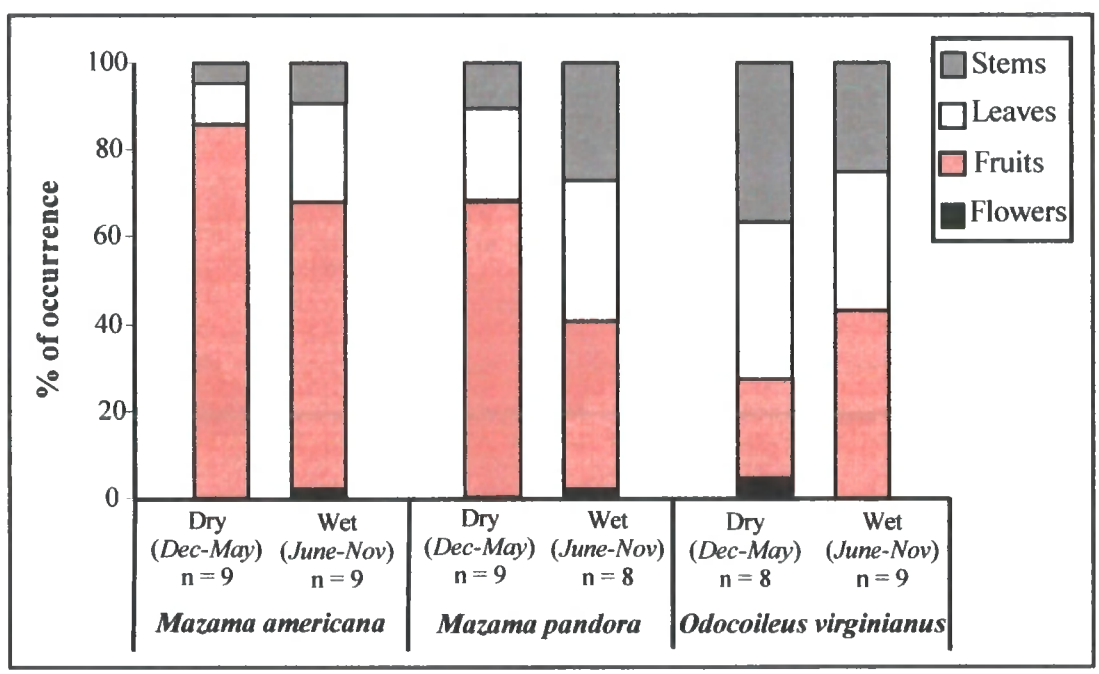

Figure 3.1. Gross seasonal diet (percentage frequency of occurrence of plant vegetative and reproductive parts) determined from the analysis of stomach contents (n = 52; *Mazama americana*, n = 18, *Mazama pandora*, n = 17 and *Odocoileus virginianus*, n = 17) in the GCR, Mexico.

White-tailed deer stomachs contained the largest amounts of unidentified plant material (47%) compared with *Mazama pandora* (33 %) and *Mazama americana* (19%). This was highly associated with the fact that more than half of the white-tailed deer samples probably came from sub-samples collected from the reticulum (therefore increased plant digestion occurred) instead of coming from the rumen and also because the browsing habits of the white-tailed deer make the identification of semi-digested leaves a difficult process (Figure 3.2).

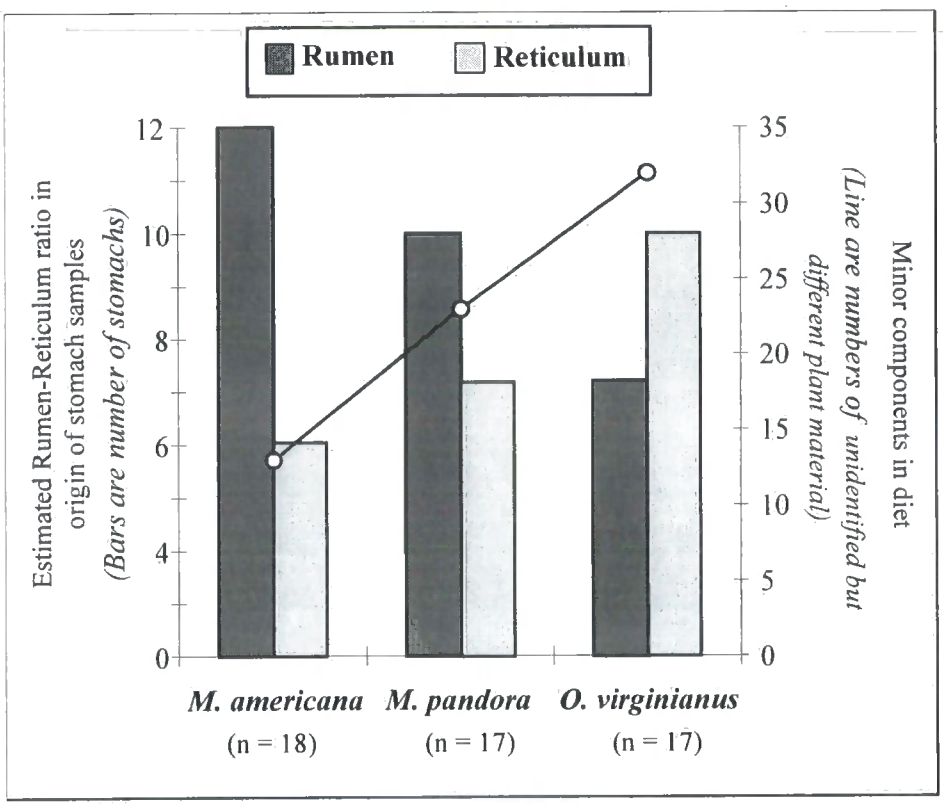

Figure 3.2. Relationship between the ratio of rumen/reticulum origin of stomach samples and the amount of unidentified plant material (minor components of very digested plant material). Diet determined with the analysis of stomach contents (n= 52) in the GCR, Mexico.

3.4.1.2. Seasonality of plant consumption

The main differences (both seasonal, in gross composition and in plant species composition) in the diet of the three species of deer were as follows: There were highly significant differences in gross composition (amounts of fruits, leaves and stems consumed) during the dry season between *Mazama americana* and *Mazama pandora* ($G = 6.72$, $df = 2$, $p < 0.05$, figure 3.3a), *Mazama americana* and *O. virginianus* ($G = 36.41$,

df = 2, p< 0.0005, figure 3.3c) and *Mazama pandora* and *O. virginianus* (G = 16.75, df = 2, p< 0.001, figure 3.3e). During the wet season, differences in gross diet composition were also significant between *Mazama americana* and *Mazama pandora* (G = 31.07, df

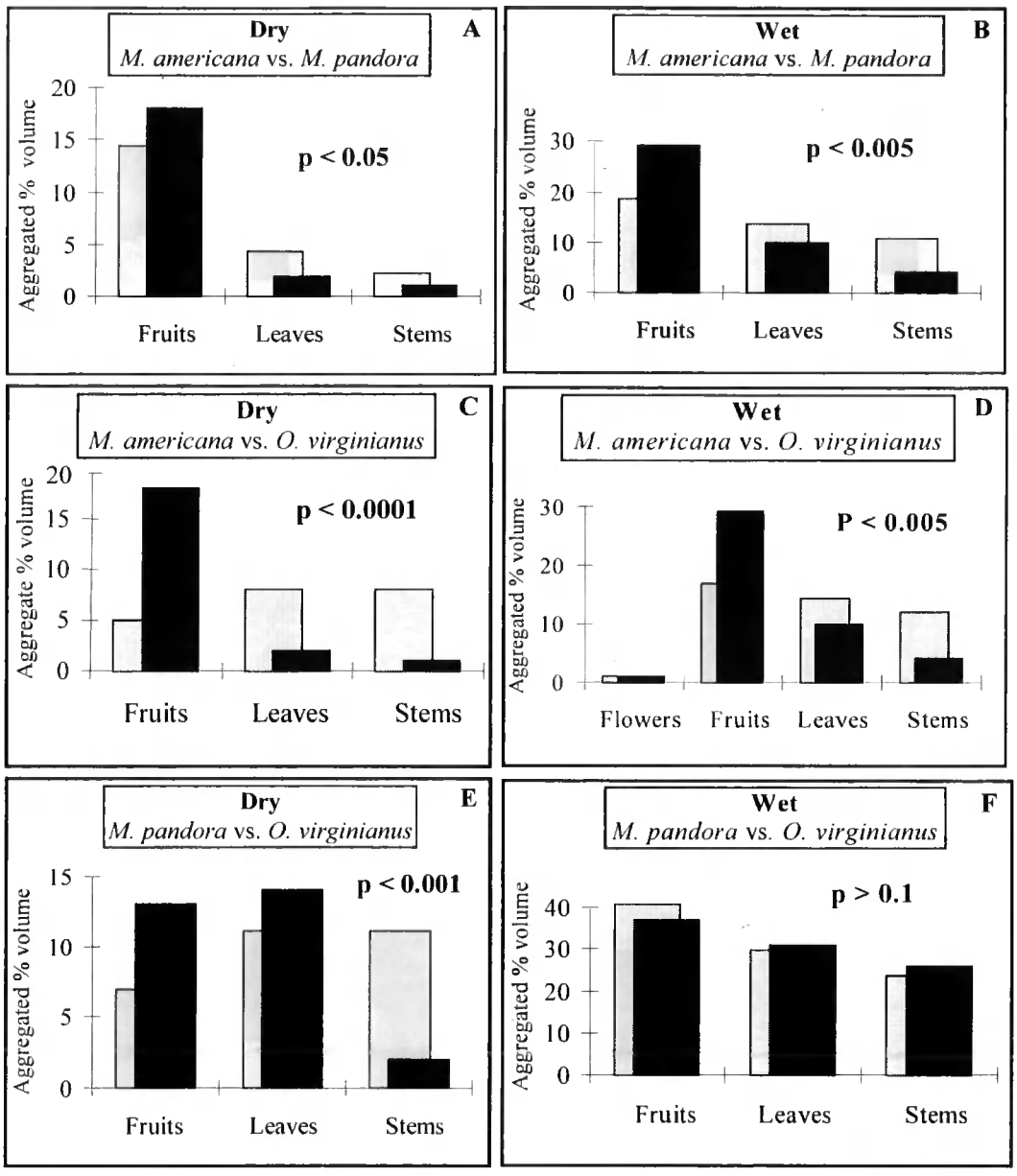

Figure 3.3. Seasonal differences in the gross diet of the three species of deer determined by analysis of stomach contents (n= 52; *Mazama americana*, n = 18, even number for the dry and wet seasons, *Mazama pandora*, n = 17, 9 from dry season and 8 from wet season, *Odocoileus virginianus*, n =17, 8 from dry season and 9 from wet season) in the GCR, Mexico. Observed (dark bars) and expected (light bars) values are represented for the log-likelihood "G" tests. Differences were considered statistically significant when p < 0.05.

= 2, p<0.005, figure 3.3b) and *Mazama americana* and *O. virginianus* (G = 11.57, df = 2, p< 0.005, figure 3.3d). Differences were non significant between *Mazama pandora* and *O. virginianus* (G = 0.66, df = 2, p> 0.1, figure 3.3f) in gross diet composition during the wet season, suggesting some diet overlap between these two species at this level.

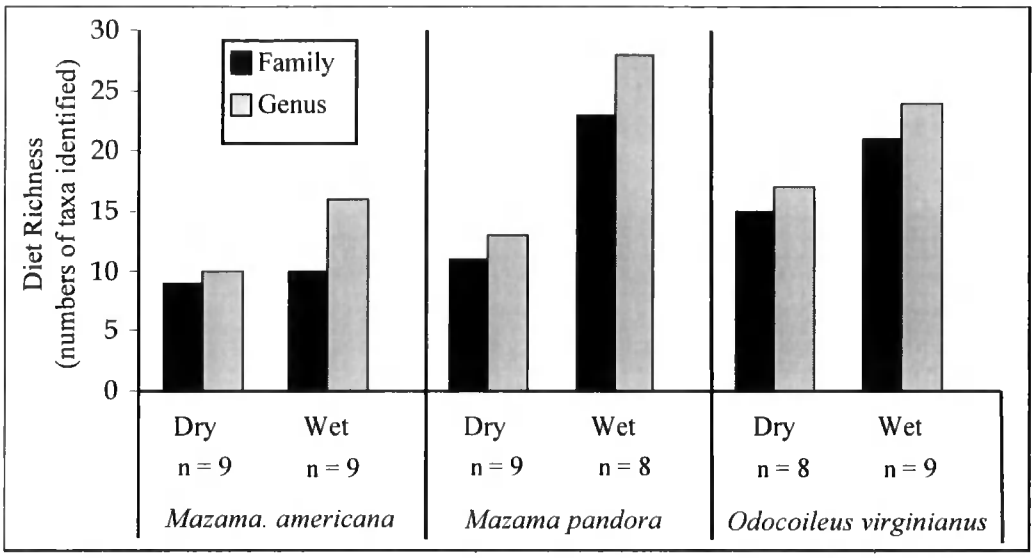

Figure 3.4. Diet "richness" of deer (number of plant taxa at the family and genus levels) determined with analysis of stomach contents (n= 52; *Mazama americana*, n = 18, *Mazama pandora*, n = 17, *Odocoileus virginianus*, n =17) in the GCR, Mexico.

Overall, the white-tailed deer consumed the wider array of plant resources available year-round (26 species from 36 available in the whole deer diet spectrum) but *Mazama pandora* consumed a largest array during the wet season. The diet of *Mazama americana* was the most specialised, consuming less than ten classes of plants (at any taxonomic level) during the dry season and between 10 and 15 during the wet season, or a total of 20 species from 46 available in the whole deer diet spectrum.(Table 3.1, Figure 3.4). These seasonal differences in the array of plant resources consumed were statistically significant at the plant family and genus levels between dry and wet seasons for the white-tailed deer (Man-Whitney tests U = 33.56, d. f. = 1, p < 0.05) and for *Mazama pandora* (U = 48.23, p < 0.01) but not for *Mazama americana* (U = 16.21, p > 0.05) (Figure 3.4).

At the taxonomic plant level, the diet of the three species of deer was dominated by five plant families from six genera and perhaps eight or nine species of plants that constitute their staple food more or less year-round (Table 3.2, Figures 3.5 and 3.6).

Table 3.1. Deer diet richness as expressed by all plant material identified to the plant family, genus and species levels in the stomach contents sampled (Total n= 52; *Mazama americana*, n = 18, *Mazama pandora*, n = 17, *Odocoileus virginianus*, n =17) in the GCR, Mexico.

	Family		**Genus**		**Species**	
	Overall	Average per stomach	Overall	Average per stomach	Overall	Average per stomach
Mazama americana	12	4.5	21	4.0	20	3.4
Mazama pandora	27	5.8	36	4.5	26	3.4
Odocoileus virginianus	28	4.9	34	3.8	26	2.9
All deer overall diet	36	5.0	55	4.1	46	3.2

The analysis of deer diet richness at the plant family, genus and species levels shows that the three species of deer present strong preferences for the *Moraceae* (*Brosimum alicastrum*), *Sapotaceae* (*Manilkara zapota*), Leguminosae (*Eugenia spp., Haematoxiulum* spp. and other species), *Lauraceae* (*Nectandra salicifolia*) *Mirtaceae* (mostly *Thebetia sp*) and *Palmae* (mostly *Chamaedora* spp. and *Sabal* spp.) (Table 3.2). However, preferences among families and species of plants varied between deer species at the taxonomic level (Figure 3.4) and also at the level of plant vegetative or reproductive portion consumed (Figure 3.6). The three deer species consumed large amounts of fruits of *Manilkara sapota* and *Brosimum alicastrum* trees through the year, but *Mazama americana* diet was largely composed of fruits of these two species (more than 75% of total annual APV) (Table 3.2, Figures 3.6 and 3.7).

According with the Johnson's rank preference indicex, the three species of deer jointly "preferred" only four families of plants from a spectrum of 36 families found composing their diet. The two brocket deer species "preferred" 9 and "avoided" 23 families of plants, while the white-tailed deer "preferred" 14 and "avoided" 17 families of plants (Figure 3.5).

Table 3.2. Johnson's rank preference indices of all the plants identified to the species level in the diet of deer for which APV was determined. Analysis of stomach contents (n= 52; *Mazama americana*, n = 18; *Mazama pandora*, n = 17 and *Odocoileus virginianus*, n =17) in the GCR, Mexico. The largest the index value the largest the preference. Zero values represent lack of use.

Species	*Mazama americana*	*Mazama pandora*	*O. virginianus*	All deer
Brosimum alicastrum	11	12	9	32
Manilkara zapota	6	7	4	17
Nectandra salicifolia	2	4	3	9
Metopium brownei	1	1	3	5
Pseudobombax ellipticum	3	1	1	5
Cryosophilla argentea	2	1	1	4
Gaussia maya	1	2	1	4
Hampea trilobata	1	0	3	4
Pseudolmedia spuria	1	3	0	4
Sabal mauritiformis	2	2	0	4
Thevetia gaumeri	0	2	2	4
Byrsonimia crassifolia	0	2	1	3
Dendropanax arboreus	1	2	0	3
Hyperbaena winzerlingii	0	1	2	3
Lysiloma latisiliqua	1	0	2	3
Pouteria amigdalina	1	1	1	3
Syderoxylum foetidissimum	0	2	1	3
Bravaisia berlanderiana	0	0	2	2
Chamaedora ernesti-augusti	2	0	0	2
Gymnopodium floribundum	0	1	1	2
Malvaviscus arboreus	1	0	1	2
Swartzia cubensis	0	2	0	2
Trophis racemosa	1	1	0	2
Agonandra macrocarpa	0	1	0	1
Amyris elemifera	0	0	1	1
Asemantha pubescens	0	1	0	1
Byrsonimia bucidaefolia	0	0	1	1
Calophylum brasiliense	0	1	0	1
Casearia emarginata	0	0	1	1
Castilla elastica	0	1	0	1
Dalbergia glabra	0	0	1	1
Erythrina standleyana	0	0	1	1
Eugenia aeruginia	0	0	1	1
Eugenia winzerlingii	1	0	0	1
Guettarda gaumeri	0	0	1	1
Haematoxylum campechianum	0	0	1	1
Jacquinia macrocarpa	0	1	0	1
Krugiodendrum ferreum	0	1	0	1
Malpighia lundelli	0	1	0	1
Pimenta dioica	1	0	0	1
Sabal mexicana	1	0	0	1
Talisia floresi	0	1	0	1
Thevetia aohuai	0	0	1	1
Xylosma flexuosum	1	0	0	1

The degree of dietary overlap (Hurlbert's standardized niche breadth) at the plant familiy level was higher between *O. virginianus* and *Mazama pandora* (0.768) than between *Mazama americana* and *Mazama pandora* (0.711) or between *Mazama americana* and *O. virginianus* (0.694) where the index indicate a middle range value suggesting little dietary overlap between these last two species of deer.

Figure 3.7 show a frequency histogram of all plant material (fruits, seeds, stems and leaves) as coming from stomach samples collected in different vegetation types for the three species of deer. The bars represent the accumulated APV per plant genera found in each sample coming from different vegetation types. Some plants were found in stomach coming from most habitat types (e.g. *Brosimum alicastrum, Manilkara sapota*) while others were found only in specific habitats (e. g. *Hampea trilobata*).

By analysing the diet in relation to the vegetation type (habitat) where deer was actually killed, it was interesting to find that *Mazama americana* stomachs contained mainly plants characteristic of Tall Evergreen forest, irrespective of where the animal was actually killed, while *Mazama pandora* and *O. virginianus* stomachs contained a broader spectrum of plant remains coming from different habitat types and vegetation associations (Figure 3.7). Of course, it is impossible to ascertain for sure if the animal was actually feeding in the habitat type where it was actually killed, so that although this analysis is informative the results should be taken with caution.

The largest similarities in the diet of the three species of deer were found in the consumption of fruits, leaves, and stems of four dominant plant families (*Moraceae, Sapotaceae, Palmaceae* and *Mirtaceae*) and seven to nine species of plants within these families. The Ramon tree (*Brosimum alicastrum*) and the Zapote tree (*Manilkara zapota*) were the dominant preferred plants in the diet of the three species of deer (Figures 3.5 and 3.6).

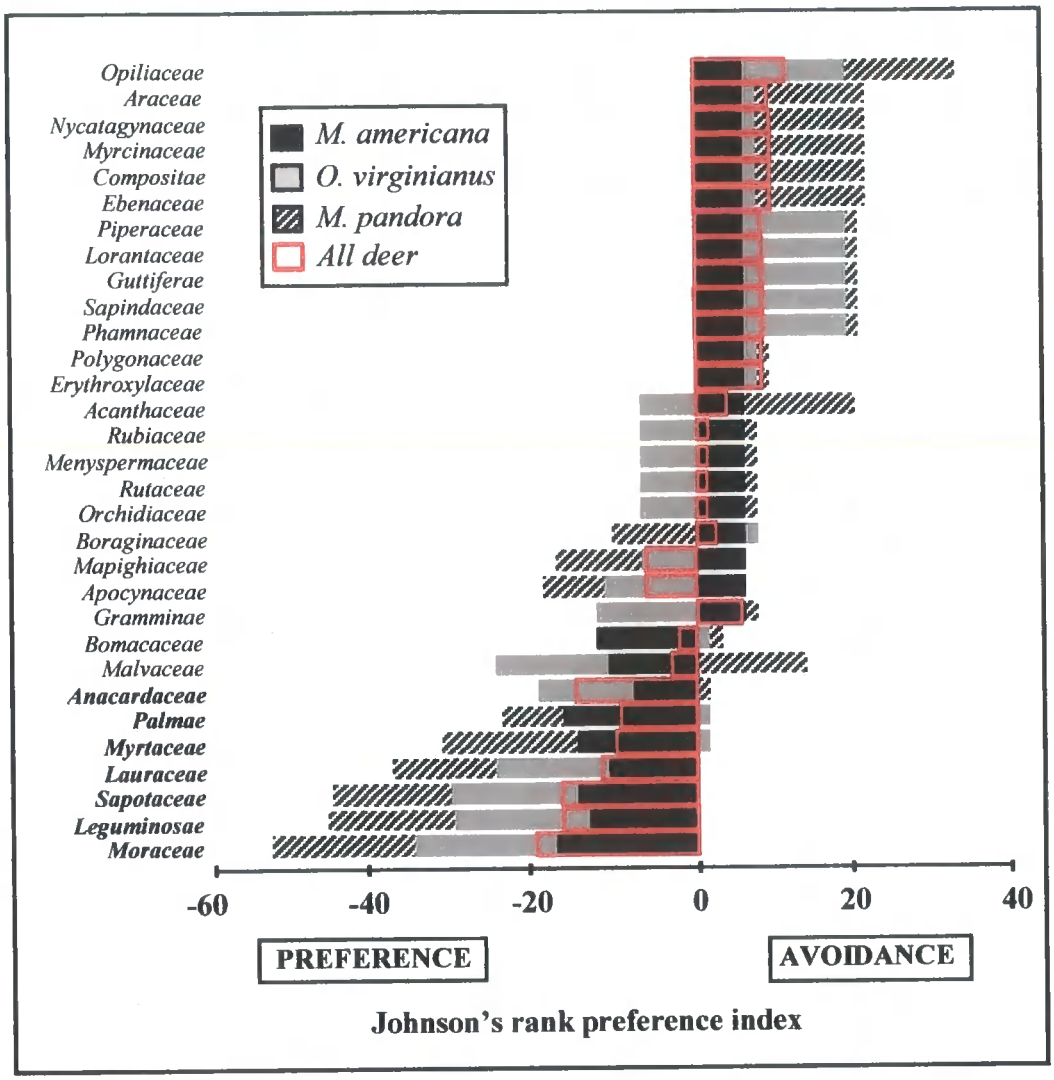

Figure 3.5. Diet overlap as rated by the Johnson's rank preference indices (JRPI) of the diet at the plant family level, determined through the analysis of stomach contents (n = 52) of *Mazama americana*, (n = 18), *Mazama pandora*, (n = 17) and *Odocoileus virginianus* (n = 17) in the GCR, Mexico. Red-clear rectangles represents the diet of all deer pooled together.

In summary, the results suggest *that Mazama americana* is a frugivore deer that depends heavily on the fruits of *Manilkara sapota and Brosimum alicastrum*. *Mazama pandora* is in the middle between a browser and a frugivore and also depends heavily in these two species of plants, but used a wider range of plant resources than *Mazama americana*. The white-tailed deer is mainly a browser and an opportunistic frugivore, consumimg the widest overall array of plant resources, but surprisingly, *Mazama*

pandora used a wider range of plant resources than *Odocoileus virginianus* during the wet season.

Two species of plants were identified as potential KPRs for the three species of deer in the GCR, based on the dominant consumption of large amounts of fruits, leaves and stems. These were the Zapote tree (*Manilkara zapota*) and the Ramon tree (*Brosimum alicastrum*). Additionally, palms of the genus *Sabal* spp. and *Chamaedora* spp. might also be considered as keystone "plant resources" for *Mazama americana* during the wet season, but their relative importance is lower than the two trees. Candidature of these plants as potential KPRs will be analysed further in the following sections.

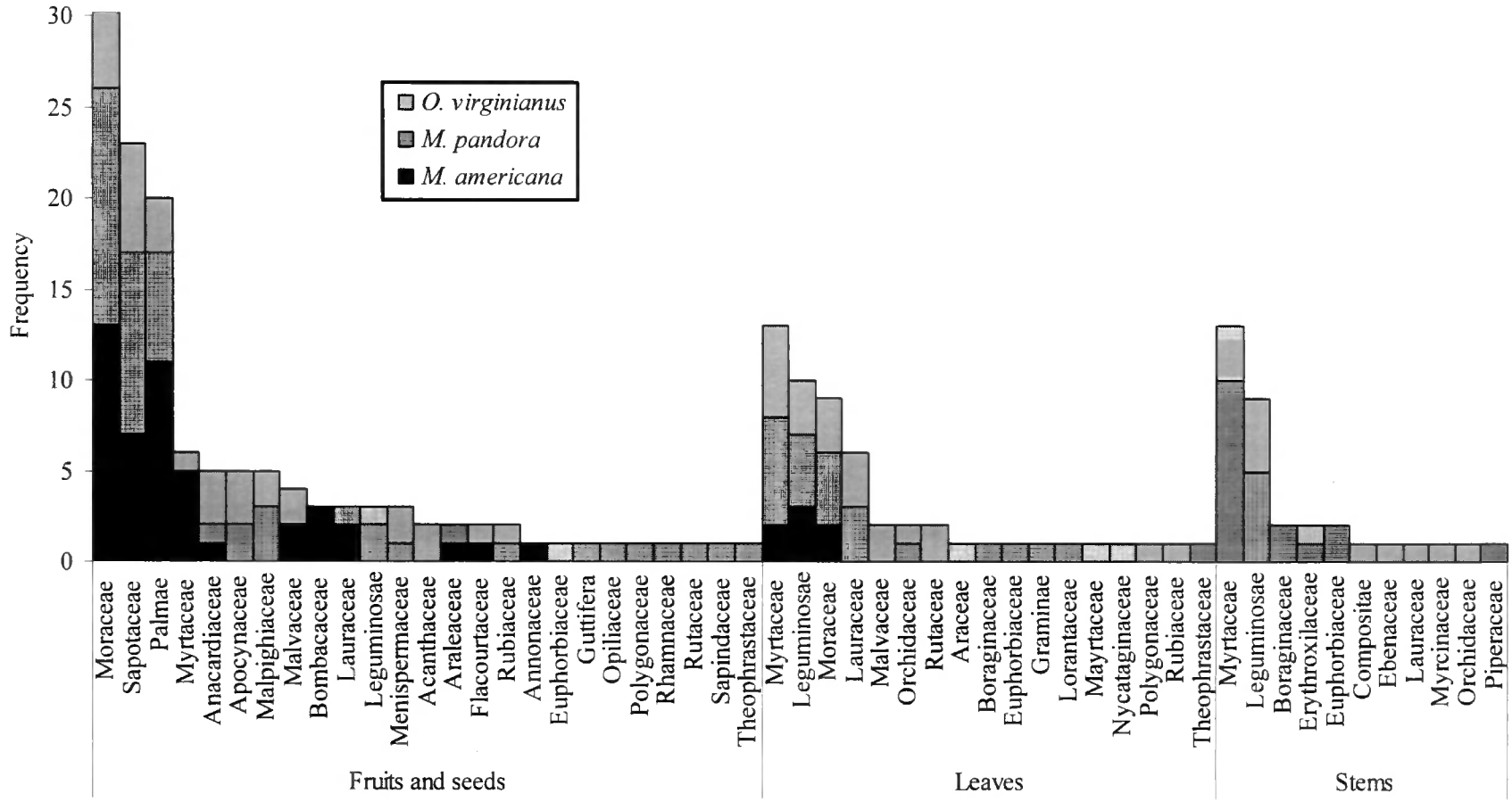

Figure 3.6. Diet of deer represented by plant families eaten and vegetative and reproductive plant portions identified in stomach samples of *Mazama americana* (n = 18), *Mazama pandora* (n = 17) and *O. virginianus* (n = 17). Bars represent number of stomachs samples.

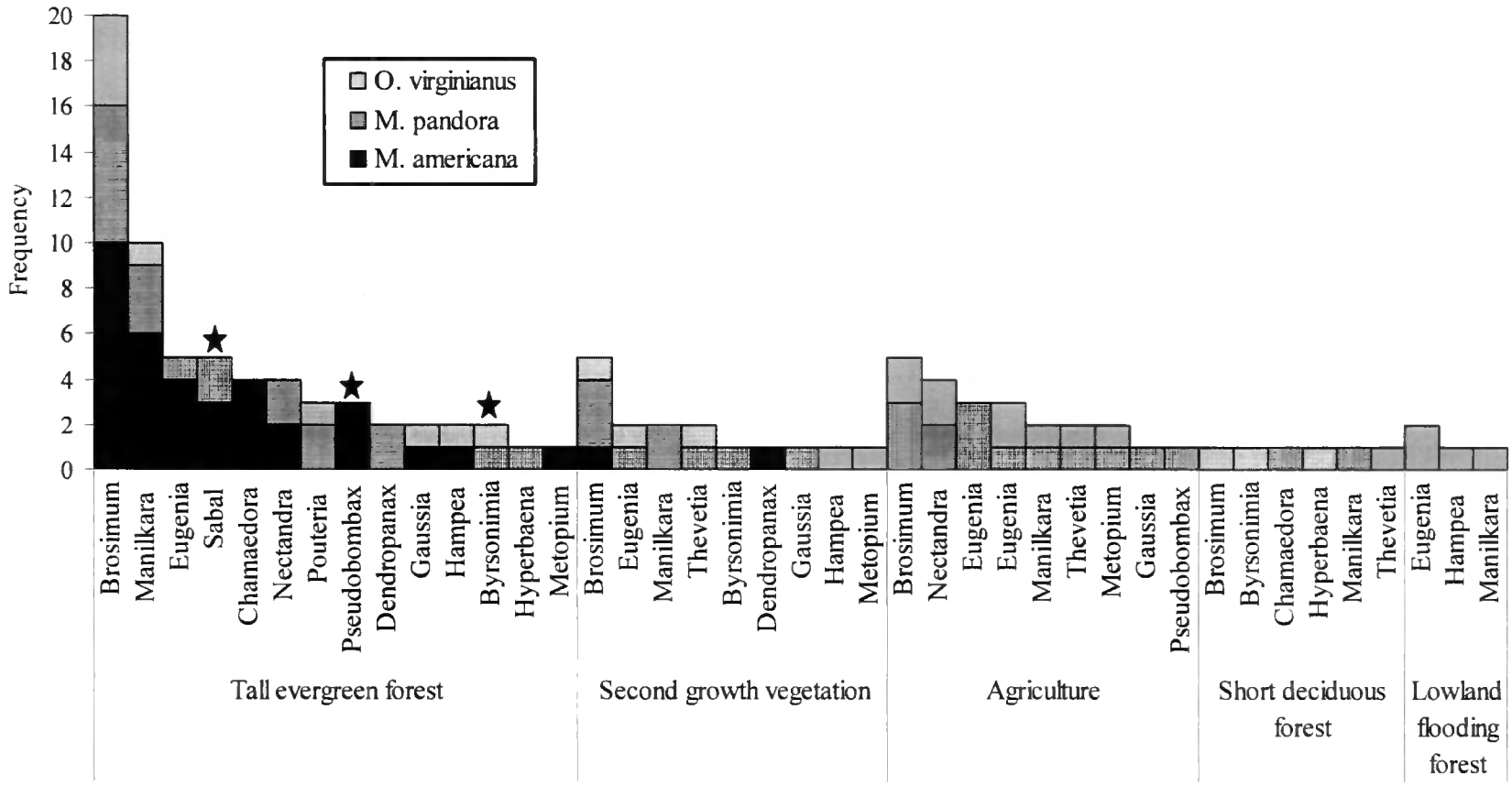

Figure 3.7. The plant genera consumed by deer in relation with habitat type (GPS location of the killing) from stomach samples of *Mazama americana* (n = 18), *Mazama pandora* (n = 17) and *O. virginianus* (n = 17). Bars represent the cumulative frequency of all vegetative and reproductive plant parts (e.g. leaves, fruits, etc) found in stomach contents. Habitats of plants are after Martinez and Galindo-Leal, (2003). ★ Represents plants found unique to a particular area in the stomach samples collected per habitat type.

3.4.2. Habitat ecology

3.4.2.1. Vegetation mapping for deer habitat types

The resulting coverage of land cover/land use re-classified from the existing coverages of Martinez and Galindo-Leal (2003) and Turner *et al.*. (2001) and composed of four vegetation associations or forest types (Tall Evergreen forest, Lowland Flooding forest, Short Deciduous forest and Second Growth vegetation) and two land use categories (Secondary Growth vegetation as a result of abandoned slash and burn agriculture fields and Agriculture) was considered highly accurate with an overall accuracy of the corresponding training points higher than 90% (Table 3.3). The highest accuracy was obtained for the Tall Evergeen forest (99%) and the lowest for the short deciduous forest (73%).

Table 3.3. Land cover and land use areas obtained through GIS analysis of the vegetation map created for the study area (Nuevo Becal). Band signal interpretation from LANDSAT imagery and comparison within the Greater Calakmul Region (GCR) are after Martinez and Galindo-Leal (2003). Comparison within the Southern Yucatan Peninsula are after Turner at al (2001) * Field verification accuracy is the percentage of field training points (n = 640 or 128 per class) that corresponded with a given vegetation classification.

	Study area Nuevo Becal landholding *(This study)*			**Greater Calakmul Region**		**Southern Yucatan Peninsula**	
Forest type classification	**Area (km^2)**	**Land cover %**	**Field verification accuracy ***	**Area (km^2)**	**Land cover %**	**Area (km^2)**	**Land cover %**
Tall Evergreen	11066	61.64	98%	8,651	36.64	12,024	70.05
Short Deciduous	0.170	2.99	73%	3,873	16.36	-	-
Lowland Flooding	3,651	21.32	98%	7,800	33.03	3,175	18.49
Total forested	14,717	85.95	-	20,324	86.03	15,129	88.54
Agriculture	1,544	9.02	99%	2,551	10.80	592	3.44
Secondary growth	0.686	4.01	89%	744	3.15	1,373	7.99
Total deforested	1,544	13.03	-	3,295	13.95	1,965	11.43
GRAND TOTAL	16,261	100	91.4%	23,619	100	17,164	100

The study area is mainly composed of two major deer habitat types: the Tall evergreen forest and the Lowland flooding forest. Together, these two vegetation classes embraced up to 82% of the pixels. The remaining land cover/land use classes had individual land cover percentages lower than 10% (Table 3.3).

The Nuevo Becal study area is still in an outstanding degree of conservation with up to 85% of the area still completely covered with continuous forest. The main characteristics, land cover/land use areas and accuracy values of the study area as compared with those from Martinez and Galindo-Leal (2003) and Turner *et al.*. (2001) are summarized in Table 3.3.

Proportionally, the new classification had similar area values for most land cover/land use classes to those originally proposed by Martinez and Galindo-Leal (2003), with the exception of the Short Deciduous forest. This vegetation class has a largest cover area in the original classification, but this is due to the distribution of this forest type in the GCR. The Short Deciduous forest occur mostly on the north and east-central portions of the GCR, while the study area is located in the west-central plateau where both Tall Evergreen and Lowland Flooding forest are dominant (Martinez and Galindo-Leal, 2003)

3.4.2.2. Forest structure and composition

As could be expected, forest structure and composition differed greatly among the three habitat types sampled. The main characteristics of each forest type are presented in Table 3.4. Tree diversity and species richness were larger in the Tall Evergreen forest, followed by Short Deciduous and Lowland Flooding forest. In general, larger tree diameters and higher trees were found also in the Tall Evergreen than in the other forest types. These differences were highly significant (ANOVA for tree diameter, $F = 3.96$, d. f. = 2, $p < 0.001$; tree height, $F = 4.63$, d. f. = 2, $p < 0.005$). Conversely, nearest distances between trees (distance to the nearest neighbour) were found in the Lowland flooding forest and the difference with the other two forest types was highly significant (ANOVA, $F = 2.84$, d. f. = 2, $p < 0.0001$). Closed canopies were also found in the Lowland Flooding forest, although this difference was only marginally significant (Kruskal-Wallis test, $F = 5.32$, d. f. = 2, $p < 0.05$).

Table 3.4. Forest structure and composition parameters in nine Canfield intercept lines located at random in three major forest types at the Greater Calakmul Region, Campeche, Mexico (3 replicates per forest type. 100 trees sampled per replicate).

Variable	Tall Evergreen forest (n = 300)	Short Deciduous forest (n = 300)	Lowland Flooding forest (n = 300)
Tree species richness	38	26	19
Shannon-Wiener diversity index (trees)	0.974	0.813	0.712
Mean tree diameter (cm) (DBH) (sd)	35.8 (12.0)	24.2 (7.34)	17.4 (6.3)
Mean tree height (meters)(sd)	23.5 (17.5)	18.5 (12.8)	12.2 (8.32)
Mean canopy density value (density)	Closed	Open	Closed
Mean distance to nearest neighbour (meters) (sd)	7.5 (3.8)	12.1 (9.4)	3.2 (4.2)

3.4.2.3. Fruiting phenology of dominant tree species

The phenology of tree species presented a characteristic double-peak fruiting period for the great majority of tree species sampled. Most species presented fruiting peak times at the beginning of the dry and at the middle of the wet seasons, but many species remained with some fruits throughout the year (Figure 3.8).

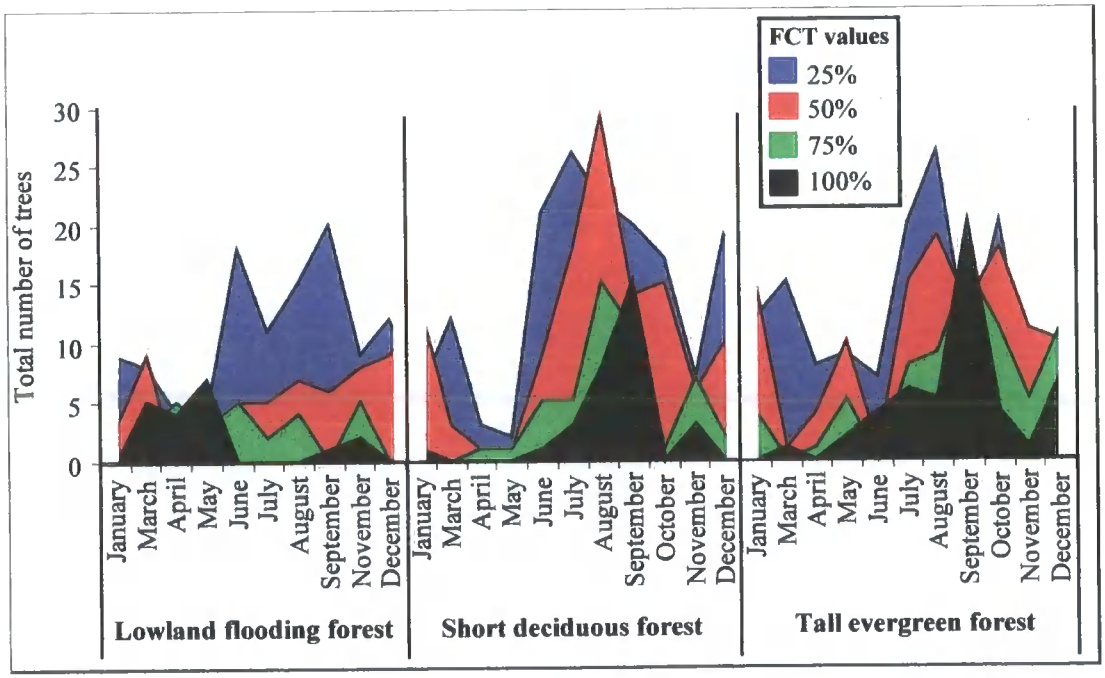

Figure 3.8. Fruit phenology represented by percentage fruit availability rates in 12 species of trees (see text) that comprise the major components of the diet of deer in the GCR, Mexico.

The main peaks in fruiting for all species sampled in the Tall Evergreen and Short Deciduous forests occurred during July, August and September when considering only 100 and 75% FCT. These peaks correspond with the core of the wet season. If 25 and 50% FCT are considered then some species presented double and even triple peaks that occurred during the dry season (December to March) in particular in the Lowland Flooding forest (Figure 3.10).

Differences in fruiting phenology among forests types were complex. While some trees in the Tall Evergreen forest and in the Lowland Flooding forest seem to remain with at least some fruits (e. g. 25% FCT) year-round, there is an almost totally "fruit-less" period during April and May in the short deciduous forest (Figure 3.8).

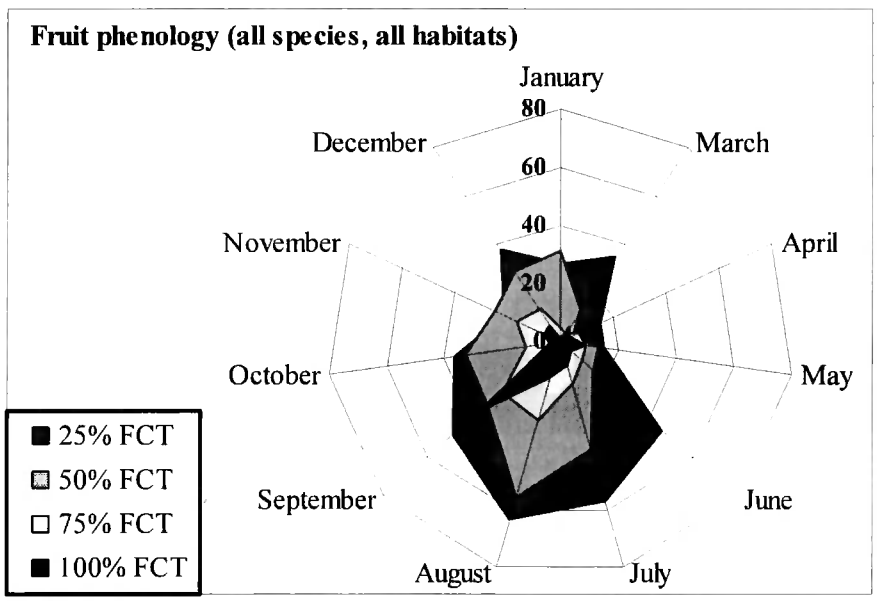

Figure 3.9. Rose diagram of the mean temporal phenological patterns of all plants of major importance in the diet of the three species of deer in all habitats sampled. The legends represent the media value of Fruit Cover on Tree (FCT). The central axis values are percentage of total number of plants sampled. Both percentages are averages of the three vegetation types sampled.

However, the intensity of the fruiting periods was different also when considering 25-50% and 50-100% FCT values. Overall for the three forest types, more than 50% of the trees presented values of 25-50% FCT during the wet season from June to September, but less than 30% of the trees presented values from 25-50% FCT during the dry season from December to March. Fruit bursts of 100% FCT occurred for a few species during August and September and periods of fruit scarcity (with less than 20% of the tress

having 25% FCT) occurred during April and May in the Tall Evergreen and Short Deciduous forests, but were compensated by some fruit bursts in the Lowland Flooding forest (Figures 3.8, 3.9 and 3.10).

Using the running mean fruiting FCT values to look at differences in fruit phenological patterns between habitat types, significant differences were found in mean fruiting times at the tree community level (Figure 3.11). Trees of the Tall Evergreen forest produce large amount of fruits during the whole of the wet season (July to November), while Short Deciduous forest species fruit during a shorter period from the end of August to the end of October (Figures 3.10 and 3.12). On the other hand, most Lowland Flooding forest tree species had their peak fruiting periods during the dry season (March to June) and had very few fruits during the wet season (Figures 3.10 and 3.12). These differences where statistically significant for the running means FCT values of the three forest types (Kruskall-Wallis test, $F = 78.52$, d. f. = 10, $p < 0.001$).

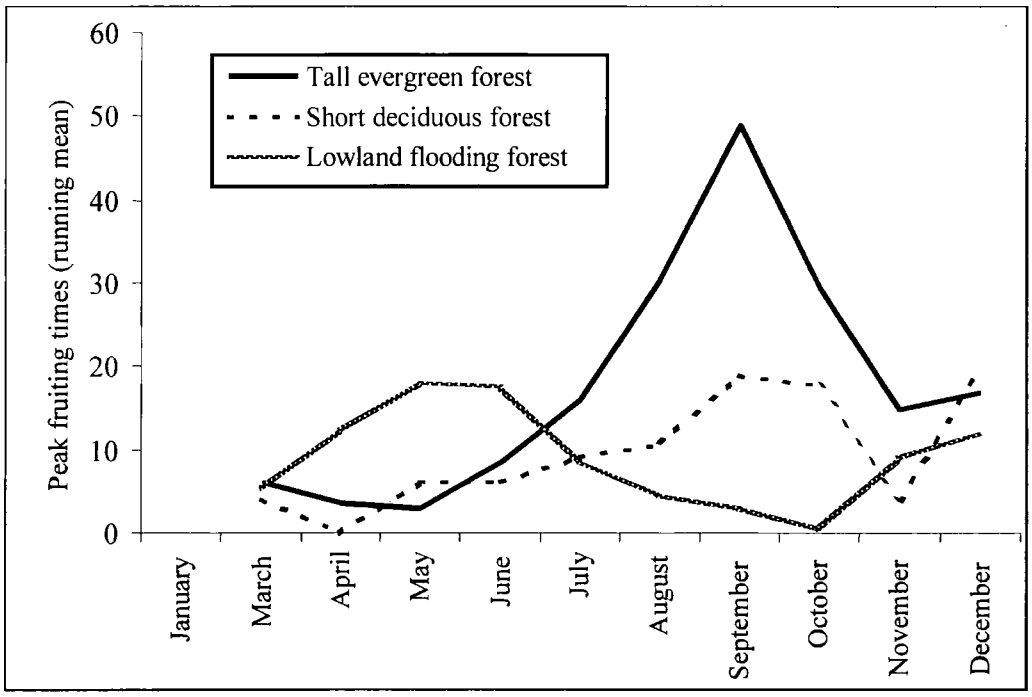

Figure 3.10. Running mean values of fruit phenology events of 12 tree species in the three major forest types of the GCR, Campeche, Mexico.

Only one species of tree (*Pseudolmedia spuria*) did not fruit at all during the year sampled and not a single tree of this species was detected with fruits either inside the phenology plots or in other visits to the forest during the whole study period of 11

months. One species, the Guayabillo (*Eugenia amigdalina* in the Tall Evergreen forest or *Eugenia sp* in the other forest types) fruited just sporadically and producing just a few but constant amount of fruits through the year and apparently with no relationship to the wet or dry seasons. Two species (*Nectandra salicifolia* and *Thebetia gaumeri*) presented just one well defined fruiting period during the wet season (June-August) and the remaining species presented the characteristic two or three-peaks fruiting pattern (Figure 3.11).

3.4.2.3. Fruit production and availability

At the species level, differences in fruiting patterns among habitats (i. e. forest types) were only detected for the Ramon tree (*Brosimum alicastrum*) (a major component of *Mazama* sp diet). This species fruited mainly during the rainy season (August to November) in the Tall Evergreen forest while fruiting was observed at the end of the wet season and beginning of the dry season (December through March) in the Short

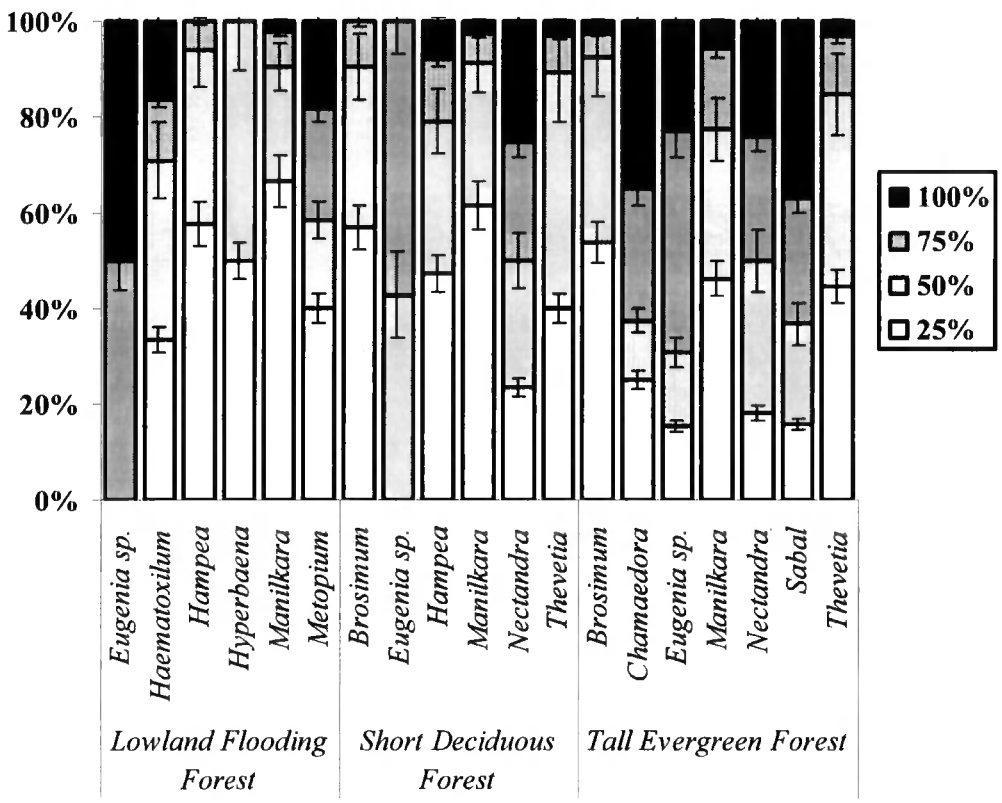

Figure 3.11. Fruit productivity (percentage of fruit cover) by forest type of the main species of trees and palms that compose the diet of deer in the GCR, Campeche, Mexico. Bars represent the percentage of trees with fruits and whiskers are one standard error. No zero values of FCT were included.

Deciduous forest. No other major differences where detected in fruiting patterns between forest types at the tree species level.

Although there is a high variability in the percentage of trees with more than 50% FCT values in the three forest types, it can be safely said that approximately the same proportion of trees (circa 30%) had FCT values 75% or higher at any given time year-round (Figure 3.8and 3.11). The remaining 70% of all trees had FCT values 50% or lower. "True" exceptions were the two palms (*Sabal* sp. and *Chamaedora* sp.) and *Nectandra salicifolia*. This last tree appears to be highly synchronized in its fruiting periods with up to 80% of the trees masting with large amounts of fruits (75% FCT and higher) during a period of 3 or 4 weeks in September in both the Tall Evergreen and the Short Deciduous forests. A "false" exception is the Guayabillo tree (*Eugenia* spp.) for which only values of 0, 50 (rare) or 100% FCT were detected in two habitat types, although most the year the trees were actually in zero fruiting phenophase (Figures 3.11 and 3.12).

3.4.2.4. Seed rain

In general terms, seed rain patterns of particular species matched closely the phenology patterns observed. However, there was a large proportion of trees that actually produced fruits but the fruits never reached the ground in the form of a seed rain, but rather in a random, scattered fashion. The amount of seeds that actually were available as seeds rain (quantifiable ratios) came from just five species (Figure 3.13) with *Nectandra salicifolia* presenting the largest seed rain/fruit production ratio index (23% in September). The remaining species presented seed rain/fruit production ratios from 4 to 17% and the timing of seed-fall was usually a few weeks after their respective fruit maturation peak (compare Figures 3.11, 3.12 and 3.13). The remaining tree species and the two palm species studied did not presented seed rains during the study period. The average seed rain ratio for the three forest types sampled and for at least 50% of the trees that presented FCT values 50% or higher was 13.5% (Figure 3.14). However, scattered major seed rain events where detected outside the phenology plots in other forest regions (in particular for *Brosimum*, *Manilkara* and *Nectandra* trees) suggesting that seed rain events might be highly regional phenomena perhaps determined by soil and other micro-habitat characteristics rather than only by phenological traits.

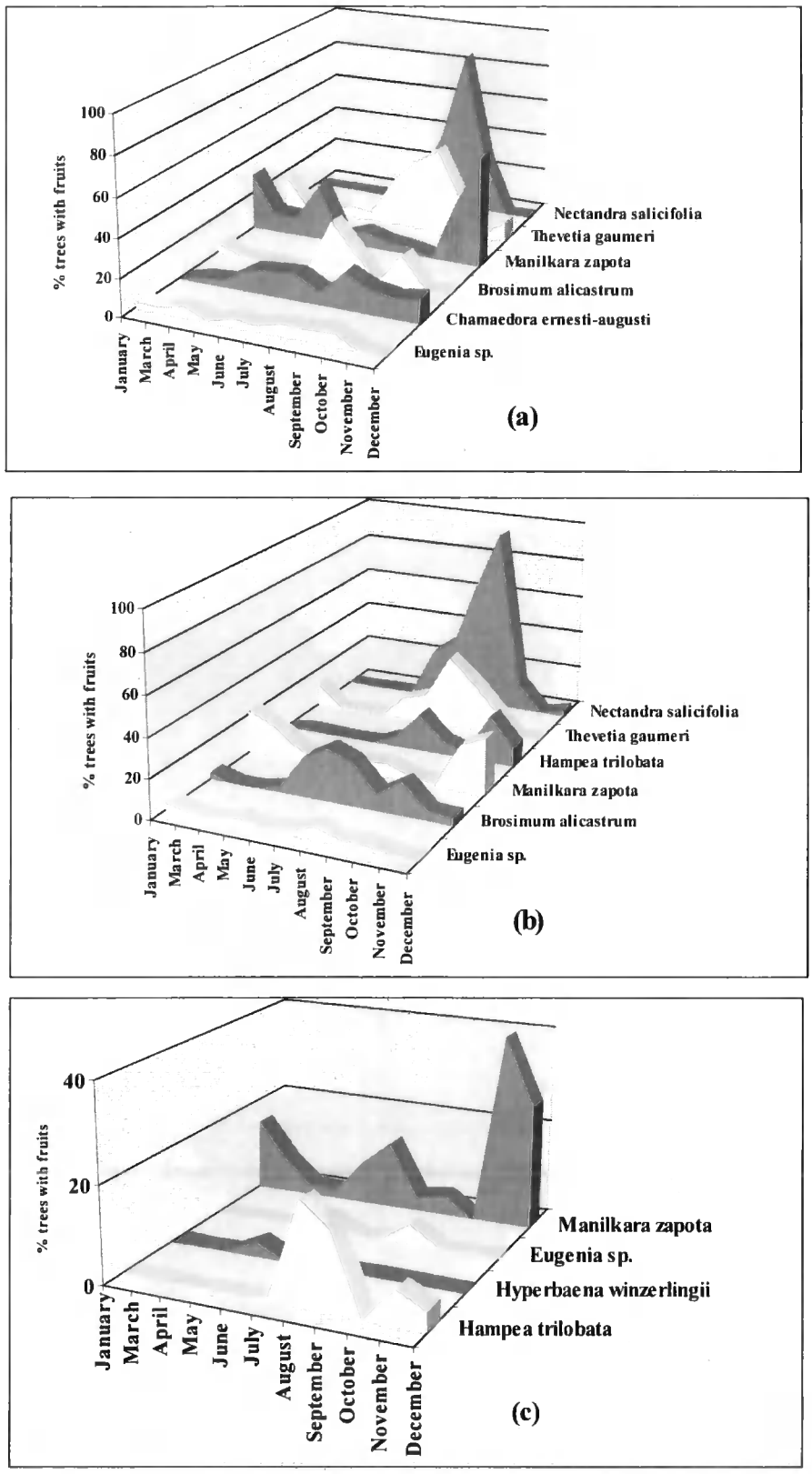

Figure 3.12. Fruit productivity (percentage of trees with fruits) of some of the main tree species sampled in the phenology plots within the three forest types sampled: (a) Tall Evergreen; (b) Short Deciduous and; (c) Lowland Flooding forests in the GCR, Mexico.

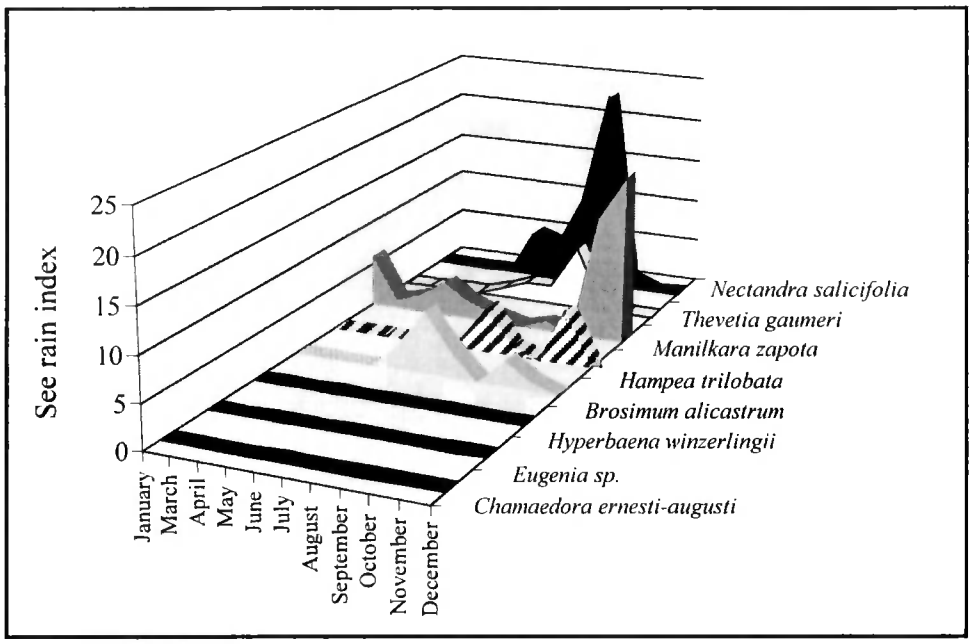

Figure 3.13. Seed rain indices (the ratio between the peak fruit phenology values and the amount of fruit available on the ground) per month in the GCR, Campeche, Mexico. *Hiperbaena winzerlingi, Eugenia spp.* and *Chamaedora ernesti-augusti* values are less than 1.

3.4.2.5. Seed predation and dispersal by deer

A total of 730 deer fresh pellet groups (585 *Mazama* sp. and 145 white-tailed deer) yielded very scarce identifiable seed remains as shown in Table 3.5. Only three semi-complete seeds were found in all the pellets examined, two were from the Xiat palm (*Chamaedora ernesti-augusti*) and one belonged to an unknown palm species. The results suggest that deer in the GCR seem to be mostly seed predators and no role on seed dispersal can be adjudicated to them, at least for seeds larger than 3 mm in size.

In situ germination experiments with these three seeds resulted in no seedlings from them (neither from stomach nor from faeces samples), therefore seed viability was considered non existent and no further laboratory work was considered necessary (Table 3.5).

Table 3.5. Results of the seed-search analysis of 730 deer pellet groups (faeces) collected from March to December 2001 in the GCR, Mexico.

	Mazama sp (n = 585 pellet groups)		*Odocoileus virginianus* (n = 145 pellet groups)	
	Number of pellets with seed remains (% of total number of pellets examined)	Seed status and percentage of seed detected as compared with a viable seed	Number of pellets with seed remains (% of total number of pellets examined)	Seed status and percentage of seed detected as compared with a viable seed
Chamaedora spp.	8 (0.9%)	6 Destroyed, 2 partially complete (10%)	2	Destroyed (10%)
Sabal spp.	3 (0.05%)	Destroyed (10%)	1	Destroyed (5%)
Thebetia spp.	3 (0.05%)	Destroyed (8%)	1	Destroyed (20%)
Moraceae	1	Destroyed (10%)	_	_
Sapotaceae Manilkara spp?	2 (0.05%)	Destroyed (10%)	_	_
Unknown palm	1	Complete	_	_

3.4.2.6. Relationships of deer abundance, diet and fruiting phenology.

Overall, there seems to be a seasonality of events related with the ecology of deer and its habitat in the GCR (Figure 3.14). Most seasonal events are linked either to the well defined wet season (July-November) or the dry season (December-May). To exemplify this, the monthly running mean values of four major sources of seasonality in the ecology of deer and their habitat were calculated as follows: deer abundance (SER), fruit availability in trees, mean fruit consumption by deer (diet) and mean fruit on-the-ground availability (seed rain) (Figure 3.14 and 3.15).

The highest abundance of deer (all three species pooled) was found either at the peak of the wet season or at the beginning of the dry season, but this difference in SER was not statistically significant (Kruskall-Wallis test, $F = 24{,}02$, d. f. = 11, $p = 0.1$).

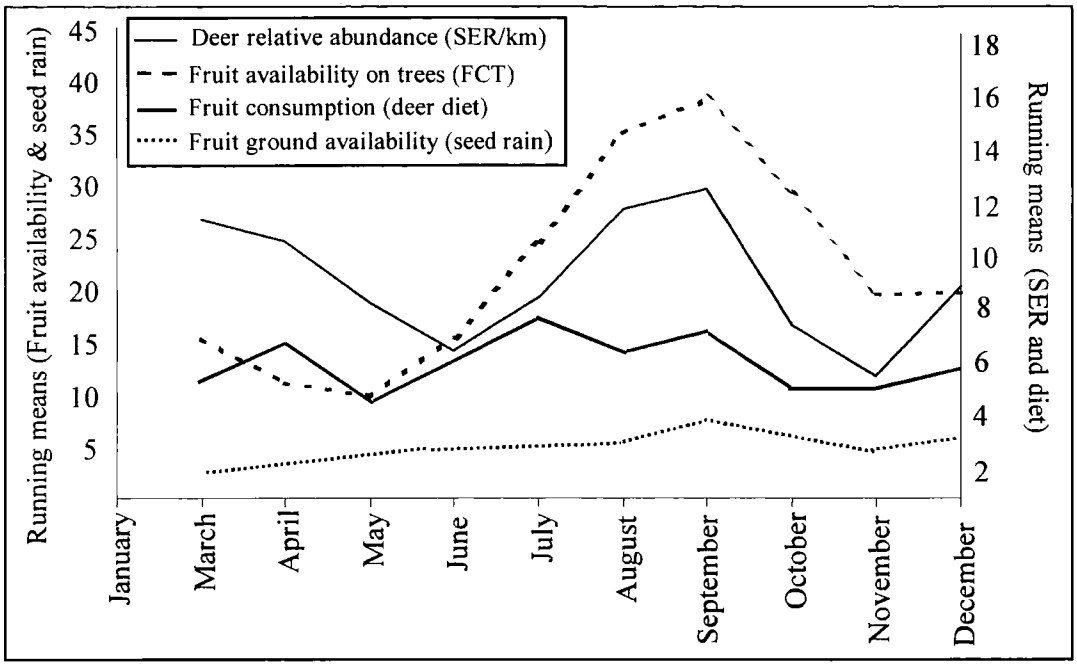

Figure 3.14. Running mean values of the seasonality of deer (all deer species pooled) abundance by sign encounter rate (SER), fruit availability in trees as determined by mean peak FCT values, fruit consumption in diet as determined by accumulated APV in the analysis of stomach contents and fruit ground accessibility as rated by seed rain mean values.

Overall mean fruit availability is strongly skewed to the wet season, but this can be considered spurious because in the calculation of the running mean, three forest types were sampled and just two of them presented fruiting periods in the wet season, while one (Lowland Flooding forest) fruited in the dry season (Figure 3.10). A similar pattern occurred with the seed rain although this trend is less clear and not as strong as with the fruit tree-availability (Figure 3.14). Because of this bias, no statistical test was applied to these running mean values other than Spearman's rank correlation coefficients. The only statistically significant correlation was obtained between the mean fruit consumption in the diet of deer and the mean seed rain values (Spearman's $r = 6.54$, $p < 0.05$, $n = 11$). All other correlations were non significant.

The seasonal diet of deer (three species combined) as represented by fruit consumption, presented well defined mean peaks at the middle of the dry season and at the beginning and the middle of the wet season (Figure 3.14). These differences (Figure 3.15) were highly significant (Kruskall-Wallis test $F = 51.23$, $df = 11$, $p < 0.005$)

Fruit availability on trees, seed rain and SER appeared to be closely associated throughout the presentation of high peaks during the wet season (August-September) and lows during the dry season (April-May) but the relationships were non-significant as mentioned earlier. However the pattern of fruit consumption remains more or less constant regardless of the other three parameters with minor peaks during March, June and August and minor lows during May, October and November (Figure 3.15).

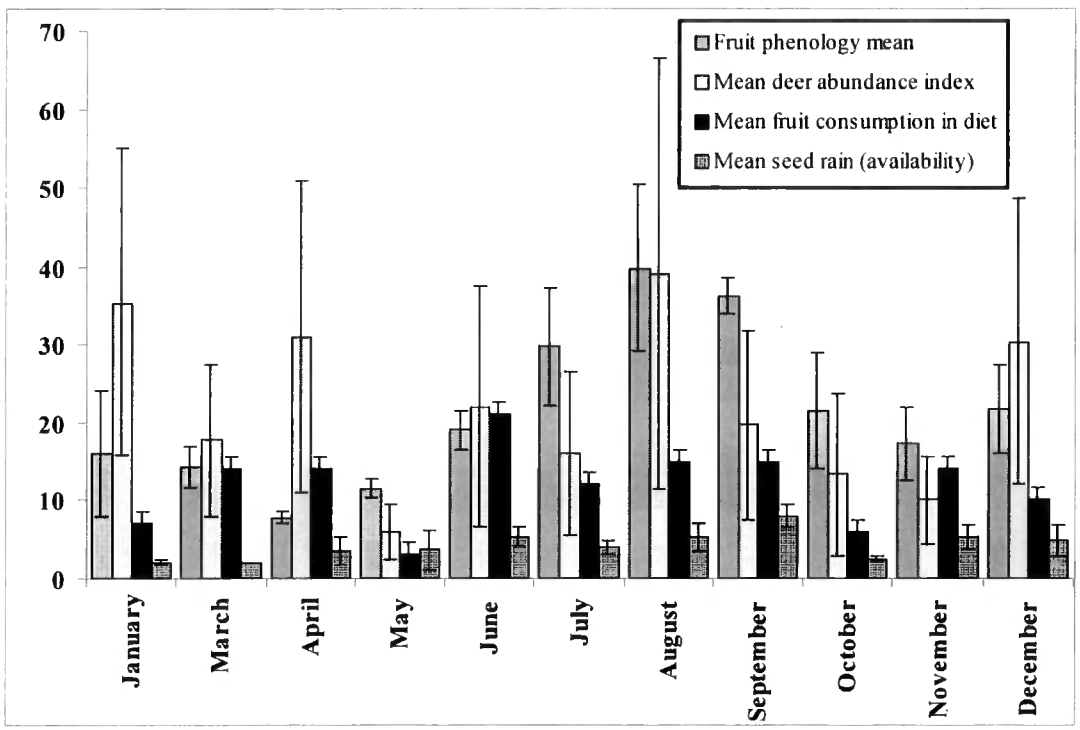

Figure 3.15. Mean and standard error (bars) of the values outlined in Figure 3.16 depicting the running mean of major seasonal ecological events of deer in the GCR, Mexico.

There were relationships in the temporal and spatial patterns of both fruiting phenology and productivity and fruit consumption (as represented by the monthly APV found in stomach samples) of eight of the most important plant species in the diet of the three species of deer. By comparing the set of rose diagrams provided in Figures 3.16 it is evident that three main patterns emerge: First, there was a three to four months almost "fruit-less" period extending approximately from February to May where a low percentage of trees (less than 30%) of these eight species had FCT values larger than 25%. However, there seems to be consumption of fruits by deer of some of these same species during these periods, at least for the Ramon, Zapote, Laurelillo and Che-Chen trees (Figure 3.16). This suggests either that other trees outside the phenology plots

sampled may had had different timings in fruit production and therefore higher availability for deer or that deer adapt to the scarcity of fruits by behavioural mechanisms such as longer feeding bouts or larger foraging areas.

Second; the temporal patterns in fruit consumption by deer closely match the temporal peak phenological patterns for the Xiat palm, the Zapote, Lecherillo and perhaps also the Guayabillo tree, but are almost completely unrelated with the other four species, remarkably the Ramon tree, a major component in the diet of deer (Figures 3.16).

An finally, third; these temporal patterns also vary among the three species of deer and the apparent temporal use that *Mazama* spp. (particularly *Mazama americana*) does of the availability of fruits seem to be superior to that of the white-tailed deer. This is evident, by comparing the matching in timings for fruit availability among the Xiat palm, Che-Chen, and Lecherillo trees and the temporal consumption peaks presented by the two *Mazama* spp. deer and *Odocoileus virginuanus* (Figure 3.16).

Identifying potential keystone plant resources (KPR) for deer.

Following Peres (2000) criteria for the identification of potential KPR, the following analysis centres in the potential role as KPR of some of the major plant components in the diet of deer in the GCR. Only three trees; the Zapote (*Manilkara zapota*), the Ramon (*Brosimum alicastrum*) and the Lecherillo (*Thevetia gaumeri*) and one palm (*Chamaedora ernesti-augusty*) were found as potential candidates to be named KPRs for the deer assemblage in the GCR. According to Peres's (1999) four main characteristics for the classification of KPRs (temporal redundancy (TR), consumer specificity (CS), resource reliability (RR) and resource abundance (RA), none of these candidates truly qualifies as a KPR. The closest being the zapote tree (Manilkara zapota) which presented very high CS, RR and RA and moderate TR values (Table 3.6).

Table 3.6. Potential keystone plant resources (KPR) and their "keystones" attributes (as defined in the literature) for deer -and possibly many other vertebrates- in the Greater Calakmul Region, Campeche, Mexico.

Plant species	Plant family[1]	Life Form[2]	Part eaten[3]	Period available[4]	Consumers recorded[5]	TR[6]	CS[6]	RR[6]	RA[6]	Sources[7]	Potential as KPR (as defined)	Potential as KPR (for deer in the GCR)
Manilkara zapota	Zap	CT	Mc, Fp	Year round	D, Pe, Ba, Mo, Bi	M	VH	VH	VH	1, 2, 3, 4, 5, 7	**H**	**VH**
Brosiumum alicastrum	Mor	CT	Wf	Jun-Dec	D, Pe, Ba, Mo, Bi	L	VH	VH	VH	1, 2, 3, 4, 5, 6, 7	**H**	**H**
Nectandra salicifolia	Lau	SCT	Mc, Fp	Aug-Nov	D, Bi	M	U	M	M	1, 2	N	N
Thevetia gaumeri	Apo	SCT	Wf, Fp	Aug-Nov	D, Ba,	L	U	H	M	1, 2, 6	L	M
Metopium brownei	Ana	SCT	Wf	Dec-Apr	D, Bi	H	VL	M	VL	1, 2, 6	N	N
Eugenia spp.	Myr	SCT	Wf	Year round	D, Bi, U	L	U	VL	VH	1, 2, 7	N	N
Chamaedora spp.	Pal	UP	Wf	Year round	D, Bi	L	U	M	L	1, 2	L	M
Sabal mauritiformis	Pal	AP	Wf	Jul-Nov	D, Bi	L	U	VL	H	1, 2, 7	N	N

1. The plants and families chosen as potential KPR were those representing the most important food resources for deer and the closest to the accepted definition of KPR according to Peres (1999). Plant families: Mora, *Moraceae*; Sapo, *Sapotaceae*; Lau, *Lauraceae*; Apo, *Apocinaceae*; Ana, *Anacardiaceae*; Myr, *Myrtaceae*, and Pal, *Palmae*
2. Life Form: CT = Canopy tree, SCT = Sub-canopy tree, UP = Understory palm, AP = Arborescent palm.
3. Part eaten: Wf = Whole fruit, Mc = Mesocarp, Fp = Fruit pulp.
4. Period available: As recorded in the present study for the GCR. Mean running FCT values on trees per month were considered.
5. As this is an auto-ecological study on tropical deer populations and very little is known on plant resource use in the GCR, much information is needed on this attribute. Consumers: D = Deer; Pe = Peccaries; Mo = Monkeys; Ba = Bats; Birds = Bi, U = Unknown.
6. Population-specific resource importance parameters following Peres (1999).Temporal redundancy (TR), consumer specificity (CS), resource reliability (RR) and resource abundance (RA), assigned to one of five categories: very high (VH), high (H), medium (M), low (L) and very low (VL), unknown (U), none (N).
7. (1) Leopold (1977); (2) this study; (3) Peres (1999); (4) Martinez and Galindo-Leal (2003), (5) Calmé, S. unpubl. data, (6) Vargas-Contreras, J. *et al.* (*in prep*), (7) Weber, M. *pers. obs.* 2001.

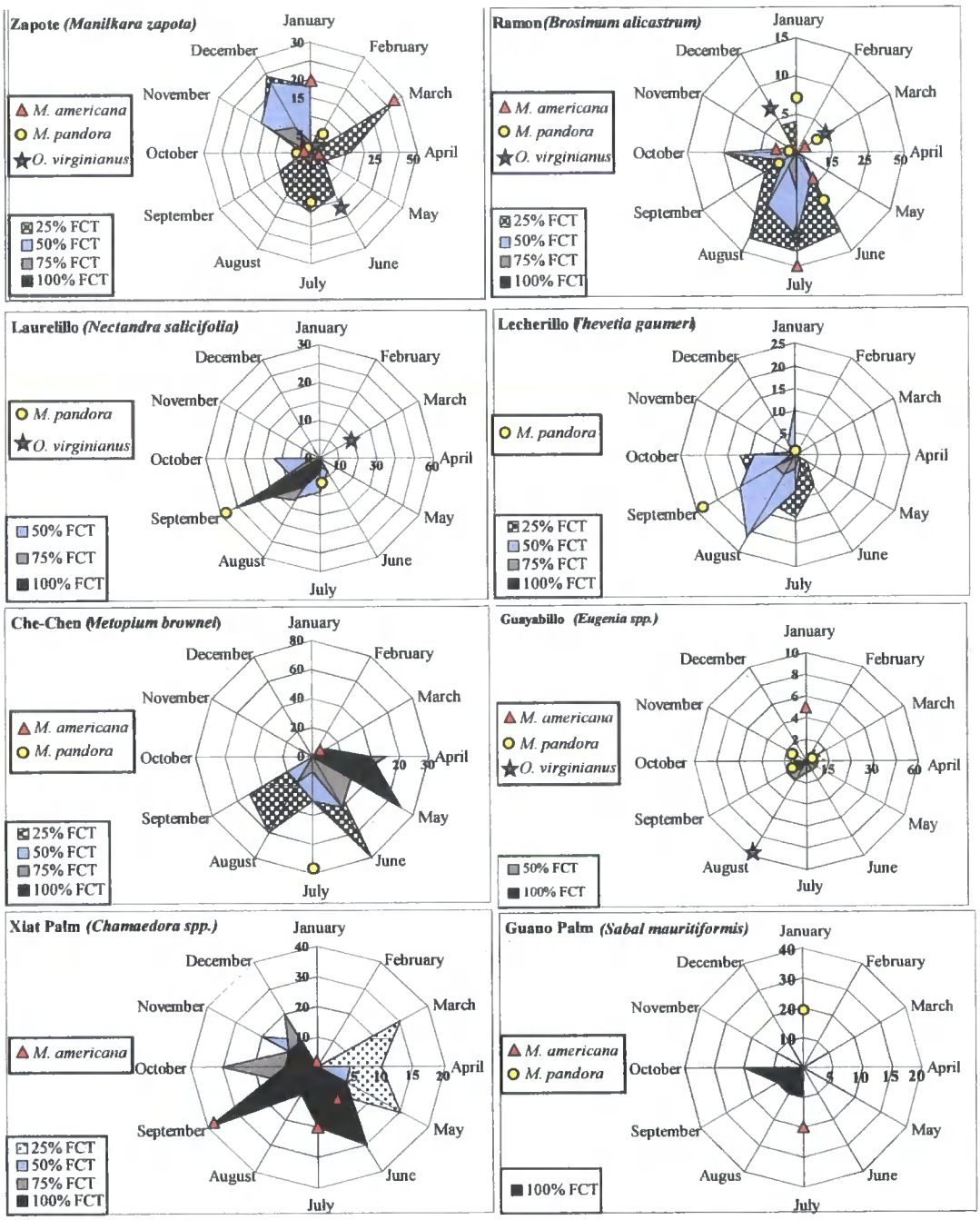

Figure 3.16. Rose diagrams of the mean temporal phenological patterns of the eight main species of plants composing the diet of the three species of deer (Fruit Cover on Tree-FCT) and temporal variations in fruit contents in stomach samples of *Mazama americana* (n = 18) , *Mazama pandora* (n = 17) and *Odocoileus virginianus* (n = 17). The vertical axis is the phenology (percentage of number of plants) and the horizontal axis is the mean aggregate percent volume (APV-bulk weight values/stomach). APV represents fruit use. An effort was made to obtain samples throughout the year, but some gaps in months exist as cooperating hunters did not hunt year-round. Missing data as follows: *Mazama americana* missing February, April, August and December; *Mazama pandora* missing February, April, June, and August and *O. virginianus* missing January, February, May and October.

3.5. Discussion

3.5.1. Deer diet composition and overlap

The overlap in foraging habits of the three species of deer found in this study can be discussed at three different levels. First, by looking at the vegetative and reproductive plant parts consumed. Second, by looking at the dietary richness as rated by the number of families, genus and species consumed and finally, by dissecting the results of the different overlap measures estimated (mainly the Johnson's and Hurlbert's indices).

It is clear from the results of this diet study that the three species of deer are well separated into different ecological niches throughout different foraging habits on the plant vegetative and reproductive portions consumed. This difference is evident between *Mazama americana* and the other two deer species but less obvious between *Mazama pandora* and *Odocoileus virginianus*. *Mazama americana* is clearly a specialist in the consumption of fruits from the Tall evergreen forest, while both *Mazama pandora* and *Odocoileus virginianus* exhibited a wider range of plant use and preferences from the available spectrum.

The methods used for the collection and analysis of stomach contents in this study presented a number constrains and difficulties that lead to an underestimation of species richness in the diet of deer: (1) The flora of the GCR has not been completely classified and many plants found in the stomachs of deer were either unknown or impossible to classify with matching herbarium voucher specimens; (2) The lack of a micro-histological plant voucher collection precluded the use of precise micro-identification techniques of plant material; (3) sub-sampling of some partial stomach contents (in particular those of white-tailed deer) lead to large volumes of highly digested and unidentifiable material that contributed to underestimation, in particular of leaves and stems and finally; (4), the fungus infestation of the deer pellet groups collected precluded further analysis of plant contents by volume or dry weight with this material. Notwithstanding this limitations, that mostly apply to the white-tailed deer because of its browser habits and the above mentioned constrains, the analysis of the diet of *Mazama* spp. was considered a precise estimate.

The increased difficulty for aging *Mazama americana* skulls and mandibles with the tooth eruption and wear technique (see Chapter 2) could be related with the diet

characteristics of this species. While both *M. pandora* and *O. virginianus* consume large amounts of rough plant material (e. g. stems, leaves) that might contribute to increased and well defined tooth wear patterns, *M. americana* eats a larger proportion of soft, fleshy fruits that might have a less impact on the wearing of its tooth. Some competition between the three species of deer might be considered apparent for the keystone plant resources identified (mainly the fruits of the trees *Manilkara sapota* and *Brosimum alicastrum*) but this happens when the availability of fruits is at its peak (wet season) so competition is probably minimized by high resource availability. Both trees can be found in most major vegetation associations in the GCR but are dominant and characteristic of Tall perennial forest that represent more than 30% of the forest cover in the study area.

The restricted use of a few plant resources and its role in periods of food scarcity point to the identification of somepotential "keystone plant resources" candidates (VanSchaik *et al.,* 1993; Peres, 1999) in the GCR. These were the Zapote tree (*Manilkara zapota*) and Ramon tree (*Brosimum alicastrum*) for the three species of deer and perhaps also the palms of genus *Chamaedora* spp. for *Mazama americana*. These KPRs might be important not only for deer but also for other forest-dwelling wildlife, both terrestrial and arboreal, during periods of famine given their widest availability and relatively high productivity. In general terms and following the definition of KPR as proposed by Peres (1999) only *Manilkara zapota* might qualify as a true KPR because it was the only plant resource with a high value of "temporal redundancy", that is; fruits of the zapote tree are mostly available when all other plant resources are scarce as food (Table 3.6). However, it is still a mystery what truly happened during the dry season of 2001 when an almost fruit-less period (of any kind including those of the Zapote tree) was recorded in the phenology plots of the Short Deciduous forest (Figure 3.9). Whether this was a "site plot-only effect" or a generalized phenomena is unknown but it is suggestive of possible acute famine periods in this habitat for the vertebrate community. The role of *Manilkara zapota* as an important KPR in the Tall Evergreen forest for possible habitat-complementarities becomes more evident.

In general, the diets of all deer were richer in plant species during the wet season and much more restricted during the dry season. This is suggestive of the occurrence of some nutritional stress during the dry season, in particular for the specialized frugivore;

the red brocket deer. While *Mazama americana* diet is composed year-round by no more than 15 species of plants, the diets of both *Mazama pandora* and *Odocoileus virginianus* can be almost twice as rich at almost any taxonomic plant level, particularly during the wet season.

Some results of this deer diet study contrast with results obtained in southern latitudes in other Neotropical forests. Branan *et al.* (1985) studied the diet of white-tailed deer and two brocket deer species (*Mazama americana* and *M. gouasoubira*) in Suriname and found a lack of dominance of single plant resources in the diets of deer. They found that fungi are an important component of the diet of *Mazama americana*, but concluded that all three species of deer behave as non-selective feeders in Suriname. Bodmer (1989, 1991) found that the diet of these same species of brockets was composed mainly of fruits (80% of diet) in the Peruvian Amazon. Similarly, a more recent study found that the diet of these species in the French Guyana is composed mainly of fruits (56% in red brockets and 68% in grey brockets) and the authors considered deer as non-selective feeders (Gayot *et al.*, 2004).

It was originally thought that the collection of sub-samples rather than full stomach contents by the hunters cooperating with the present study may have had an effect over some of the results obtained. While this may be true at some extent, the similarities in diet richness at the plant family, genus and species levels with the data provided by Branan *et al.* (1985) and Gayot *et al.* (2004) suggest that the effect might had been minimal. Branan *et al.* (1985) found that the diet of red brocket contained at least 57 plant species in 36 families and an average of 4 plant species per brocket and 3 per white-tailed deer stomach collected. While the overall species richness in the diet of Suriname deer is greater than that found in the present study, this is probably the result of a higher plant diversity available, since it is a well know fact that plant diversity decreases with latitude in Neotropical forests (Gentry 1982). The diet richness per stomach sample was remarkably similar to that found in the present study, again suggesting that the drawback of collecting reticulum subsamples rather than full stomachs had minimal effects. However, Gayot *et al.*. (2004) found a comparatively richer diet composition in the French Guyana deer with an average of 93 (8.6 per stomach sample) plant species found.

Overall plant diversity in French Guyana is higher than in Suriname (Gentry, 1982) and at least an order of magnitude higher than in the Yucatan Peninsula, Mexico, therefore availability to a wider diversity of plant resources might be responsible for the generalist foraging feeding habits found in brocket and white-tailed in these two previous studies. Thirty-eight species of trees were found in 100 meter long transects (Candfield lines) in the GCR (Table 3.4). A figure of three times this diversity can be easily found in tropical forests at the latitudes of French Guyana and Suriname (Gentry, 1982).

This idea is supported by a study on *M. gouasoubira* feeding habits in a less diverse and more seasonal habitat (Boreal Chaco, Paraguay) where seasonal dominance of a few plant resources (e. g. fruits of three species of plants) in the diet was found (Stallings, 1984). The diet of white-tailed deer in seasonal, temperate environments is also dominated by a handful of seasonally available resources (e. g. oak acorn masts) (Hanley, 1997).

The degree of overlap in the diets of deer is greater between *Mazama pandora* and *Odocoileus virginianus* than between *Mazama americana* and the other two species. Again, this suggests that some competition might occur between the former two species when availability of resources is limiting (e.g. dry season) more often than competition with *Mazama americana*. The separation of deer throughout different habitat use patterns supports this hypothesis (Chapter 2). To the best of my knowledge no study had ever measured the degree of dietary overlap for small, forest-dwelling ungulates in Neotropical forests. Bodmer (1989, 1991) investigated the frugivory role of the assemblage of ungulates in the Peruvian Amazon, but does not discuss dietary overlap. Hoffman's classification of ungulate feeding habits, rates the *Mazama* genus as a "concentrate selector" and the white-tailed deer as "intermediate" between a concentrate selector and a "bulk feeder" (Hoffman, 1985). The results of this study clearly point out that we have to be careful with this broad classifications, since the feeding habits of *Mazama pandora* and *Odocoileus virginianus* were actually closer than the feeding habits of the two *Mazama* species. Therefore, according with Hoffman' s classification, both *Mazama pandora* and *Odocoileus virginianus* could be rated as intermediate species and *Mazama americana* as a concentrate selector, leading to an even more

general classification of "generalists" for the first two species and "specialist" for *Mazama americana* according with their feeding habits in the GCR, Mexico.

Dietary switching appears to be the most important of all the possible behaviours that serve to mitigate the impact of scarcity of food resources in tropical forests (Van Schaik *et al.*, 1993). During periods of scarcity, many herbivorous mammals resort to feeding on materials that; (i) are of low nutritional value (e.g. some vegetative portions of the plants such as stems) (ii) are protected by hard coverings, which increase handling time (e.g. palm nuts), (iii) contain chemical deterrents, that can be ingested (such as tannins) or (iv) are randomly distributed in the environment, such as more time must be invested in searching (e.g. nectar) (Terborgh 1983, Van Schaik *et al.* 1993). The opportunities for dietary switching of this kind are closely tied to phenological patterns, depending for example, on whether the two categories of the food resources vary in relation to the seasonal cycle. The role of dietary switching can be important to further corroborate if competition for scarce available resources occur between *Mazama pandora* and *Odocoileus virginianus*. This study strongly suggest that maybe competition is likely to occur, particularly during the wet season when the diets of these two species are remarkably similar and therefore overlap considerably. Whether dietary switching occurs or not in the three species of deer studied is unknown and it was impossible to determine given the relatively small sample of deer stomachs collected. Further studies are needed to verify if dietary switching might be playing a role in the complex trophic interrelationships of deer and their plant resources in the GCR.

3.5.2. Habitat ecology

3.5.2.1. Vegetation mapping for deer habitat types

The vegetation mapping approach followed in this study took advantage of extensive available land cover/land use GIS resources for the GCR and southern Yucatan Peninsula areas. This was a major advantage for the present study, because this kind of landscape mapping can be extremely expensive, time consuming and technologically dependent on very specialized expert knowledge (e. g. both GIS and botanical expertise).

The decision to broaden the available land cover/land use classifications to what it was called "major deer habitat units" was successful since no data was lost and the

percentage accuracy of the vegetation classes against field verification points was high. The only exception was the Short Deciduous forest type where relatively low accuracy was obtained. It is important to note one major difference in the vegetation classification systems of the coverages used in this study. While both Martinez and Galindo-Leal (2003) and this study considered the Short Deciduous forest as a valid vegetation class, Turner *et al.* (2001) does not include this vegetation class and as a result their total area covered by Tall Evergreen forest is proportionally larger. However, the values provided in Table 3.3 and coming from Turner *et al.* (2001) correspond to a much larger area of the southern Yucatan Peninsula and therefore the proportional coverage per land cover/ land use category change considerably (Table 3.3).

The degree of overlap between Short Deciduous forest and Second Growth vegetation from the band four of the infra-red spectrum of the satellite image can also be responsible for the relatively low levels of accuracy in these two vegetation classes when compared with the highest accuracies obtained for Tall Evergreen and Lowland Flooding forest (Turner, B. J. personal communication 2002).

Nevertheless, the proportion of short deciduous forest in the study area (Nuevo Becal) is minimal (< 3%) when compared with the other major forest types. Moreover, the number of deer data records (e.g. stomach samples, GPS points, etc.) coming from this habitat type are also proportionally smaller. Therefore, the lower accuracy values obtained for this forest type in the new deer habitat vegetation classification may have limited effects in the overall accuracy and interpretation of spatially explicit results.

3.5.2.2. Forest structure and composition

The forest structure and composition of the three major forest types in the study area differed considerably in tree species diversity, forest height and both canopy and under-story cover (Table 3.4). This was an expected result since these forest types are readily identifiable by their physiognomic characteristics, composition and structure within the GCR (Martinez and Galindo-Leal, 2003). Moreover, this further emphasize the results obtained on the mapping of deer habitat types from satellite image-based coverages, over the fact that these vegetation classes are extremely different and can be well differentiated.

Martinez and Galindo-Leal (2003) defined the Tall Evergreen forests for the GCR as those communities where dominant trees reach heights between 15 and 25 meters, at least 75% of trees are perennial and present the highest overall tree species diversity. They define Short Deciduous forests as communities were tree height is less than 15 meters and were more than 75% of trees are deciduous. Their definition of Lowland Flooding forests describe this vegetation class as a community where seasonal floods occur during the wet season, tree height ranges from 4 to 8 meters and usually exhibit semi-perennial leaf characteristics (Martinez and Galindo-Leal, 2003).

The average tree height in the Lowland Flooding forest was larger (12.2 meters) than that provided as reference values by Martinez and Galindo-Leal (2003) but in general the results of the forest structure and composition of the forest types within the study area, closely match these definitions.

Tall Evergeen tropical forests are one of the tallest and richest in tree species diversity over the whole distribution of neotropical forests (Gentry, 1982). Short Deciduous tropical forests are more characteristic of dry tropical forests than of humid rain forests (Gentry 1982; VanSchaik *et al.*. 1993). The GCR is considered by many as a transitional area between wet tropical rain forests and dry tropical forests with morphological and physiognomical characteristics belonging to both biomes (Miranda 1958; Pennigton and Sarukhan 1998; Martinez and Galindo-Leal 2003). According with this results and those from mapping the vegetation and habitat types, the study area within the GCR might be closer in forest structure and composition to a true tropical rain forest than to a dry tropical forest. The seasonality in events, specially fruit phenology, tell a different story however.

3.5.2.3. Fruiting phenology of main plant species in deer diet

Flowering and fruiting patterns in tropical trees are influenced by biotic, climatic and edaphic factors and can be extremely complex in their presentation, timing and seasonality (Borchert, 1994; Reich 1994, Loubry, 1994). Most tropical trees produce new leaves and flowers in bursts rather than continuosly, and most tropical forest communities display seasonal variation in the presence of new fruits (VanSchaik *et al.*, 1993; Reich 1994).

This discussion of the results of the fruit phenology sampling will be directed to the usefulness of phenological studies for assessing fruit availability for primary consumers in specific locations.

The results of this study demonstrate that fruiting phenology is a highly seasonal event in the GCR where most trees fruit in small, irregular bursts during the whole of the wet season (June to October) and even smaller and more irregular bursts occurring during a more constrained period of two or three months (December to March) during the dry season. It was also demonstrated that an almost complete fruit-less period occur in at least one forest type (Short Deciduous forest) for a period of at least two months. If small percentages of trees found with less sizeable amounts of fruits (e. g. < 50% FCT) are considered, then fruiting phenology in the study area might be considered as non-seasonal.

Several studies on fruiting phenology indicate that there are variations in the temporal, spatial, inter- and intraspecific patterns of fruit production among tropical trees (Hart, 1985; Heideman, 1989; Forget, 1992; Murali and Sukumar, 1994; Madeira and Fernandez, 1999). Reproductive patterns in tropical forests range from continuous flowering and fruiting through predictable annual production to less predictable patterns (Van Schaik *et al.*, 1993, Newstrom *et al.*, 1994; Chapman *et al.*, 1999). Duration, frequency and intervals of fruiting episodes differ among trees of different successional status. According to Denslow (1980) and Bazzaz and Pickett (1980), pioneer species produce fruits every year and have extended fruiting periods. In contrast, primary forest species generally have irregular fruiting periods and may experience masting (Van Schaik *et al.*, 1993; Reich, 1995).

Williams-Linera (1997) found that fruiting is concentrated between April and November, coinciding with the dry-warm and the wet-warm season in the Gulf of Mexico (Veracruz) and concluded that phenology of tropical trees at this latitude has climate as both ultimate and proximate regulating factor. Bullock and Magallanes (1990) found that most fruiting occurs from November to April in the Pacific dry forests of Jalisco, Mexico and concluded that water availability is a major factor for the presentation of phenophases.

The location of the phenology plots in this study might have had an influence in the phenological patterns exhibited by the trees sampled in this study. The major criteria for choosing the location of the plots was that the areas were representative of the forest types sampled and that human disturbance could be minimized during the length of the sampling period (11 months). This is important because disturbance can greatly affect fruiting phenology patterns in tropical forests (Johns, 1988; Muhanguzi *et al.,* 2003). For example, according to Bawa *et al.* (1990), logging is one of the forms of forest disturbances that affects fruiting patterns in tropical forests because it alters the microhabitat and distribution of conspecific trees, consequently influencing fruit and seed production.

Forest structure and composition also affects the phenology of trees. In Belize, larger trees flushed leaves earlier than small ones in three species, and small trees flushed leaves more rapidly in two other species (Sawyer and Newberry, 2003). The way researchers measure tree phenology, therefore has an strong influence in the appreciation of seasonality (Van Schaik *et al.,* 1993). While some studies consider a small amounts of fruits as a "fruiting episode" (Guevara de Lempe *et al*; 1992; Justiniano and Fredericksen, 2000; Bawa *et al.*, . 2002) others scale their values so that more quantifiable appreciations can be performed (Newstrom *et al.*, 1994; Chapman *et al*; 1999; Hamann, 2004). It is difficult to ascertain with a reliable amount of confidence if the results of this fruit phenology study can be extrapolated to the whole GCR because of the high habitat heterogeneity exhibited in the region, but evidence of this will be discussed later.

3.5.2.4. Fruit production and availability

Overall, most tree species sampled presented a relatively low fruit productivity when compared with results obtained in other more humid and therefore more productive tropical forests. Humid tropical forest trees tend to be more productive in total fruit biomass than dry tropical forests (Van Schaik *et al.,* 1993).

On average, less than 30% of all trees sampled were found with large amounts of fruits (50% FCT or higher) at any given time. However, some trees of some species remain fruiting more or less year-round and presented bi-modal and even tri-modal fruiting

episodes, while others (remarkably *Nectandra salicifolia*) presented one single fruit burst during the year.

Bullock and Ortiz-Magallanes (1985) found that at any given time, a maximum of 30%, but usually between 10 and 20% of all trees present fruiting bursts of sizable magnitude in the Chamela Biological Station, Pacific Coast of Jalsco in the Northeast of Mexico and the reviews of other phenological studies elsewhere by VanSchaik *et al.* (1993) and Reich (1994) confirm this finding as a general pattern in tropical forests.

3.5.2.5. Seed rain

Seed rain, as defined in the present study, closely followed the periodicity in fruit phenology patterns observed in the trees. This is an interesting result because it is suggestive that for further studies in the GCR, following fruit phenology patterns in time and space can be interpreted as directly proportional to the on-ground availability of fruit biomass.

However, this has to be interpreted carefully, because the ratios of seeds available on the forest floor are usually smaller than the availability of fruits hanging on the trees (average ratios of 10-15% were found when 50% of all trees presented 50 % or higher FCTs). This basically means, that if we found a tree with 100 fruits, there will be a high probability to find between 10 and 15 fruits available on the forest floor immediately adjacent to the parent tree.

A search of the literature was unsuccessful in finding a comparable study that used a similar methodology for comparing seed rain and fruit phenology patterns. Seed rain has been traditionally measured with the use of seed traps with the rationale of making sure that all seeds captured actually come from the parent tree sampled (Mandujano *et al.*, 1994; Houle, 1995, Clark *et al.*, 1999, Curran and Leighton, 2000). This is important for some plant recruitment and seed dispersion studies, but irrelevant if the interest is in obtaining crude but accurate estimates of seed and fruit available in the forest floor for the use of ground-dwelling primary consumers.

3.5.2.6. Seed predation and dispersal

The results of seed search and retrieval in deer pellet groups demonstrated that deer are seed predators in the tropical forests of the GCR. A large number of fresh pellet groups possibly belonging to the three species of deer were collected and just a minimal amount of seed material was recovered from them. From this material, all seeds were structurally damaged and not a single germination occurred. This concurs with other studies in the Peruvian Amazon (Bodmer 1989) and in French Guyana (Gayot *et al.* 2004) where deer of the genus *Mazama* had been found predating on seeds rather than having any role in seed dispersal. The longevity and germination patterns of tropical seeds is highly variable (Vazquez-Yanes and Orosco-Segovia, 1993).

The highly effective digestive system of ruminant ungulates ensures that even the roughest of seeds can barely withstand the mechanical and microbiological digestive process taking part on the stomachs of these species (Hoffman, 1995). The role of deer in the GCR from a frugivory point of view can now be studied as one of a seed predator. The fact that search for only big seeds (>3 mm) was performed might have limited the hability to find small viable seeds in this study.

3.5.2.7. Spatial and temporal relationships of deer abundance, diet and fruiting phenology.

The spatial and temporal relationships between deer abundance, diet and fruit phenology found in this study are quite unique by the way they were determined and assessed.

Monthly samplings of deer abundance based on SER were strongly linked with peaks of higher abundance during the main fruiting season and therefore main fruit availability season.This can be explained from different perspectives. There can be a bias in the detectability of deer signs during the wet season, because the rain and therefore higher humid ground conditions allow for a higher detectability of deer signs, particularly deer tracks. However, other studies have found no statistical differences in detectability of deer and (other wildlife) tracks during the dry and wet seasons (Carrillo *et al.*. 2000, Weber, 2000, Reyna-Hurtado, 2003). Morover, the count of SER included sightings, deer trails (or pathway) as well as tracks. The former two are probably less affected than

tracks by the ground humidity conditions. Therefore, it is assumed that the detectability of deer signs was equal during the wet and dry seasons, resulting in no biases in the estimation of deer indices of abundance . Therefore, the result might be interpreted as deer abundance, as estimated by SER, is associated to food availability. This indeed, might be interpreted as a local, temporal response of deer to the increased available food resources with increased mobility (therefore more detectability) or as more generalized pattern were deer respond to the increased food supplies with a food-dependent increase in population size.

This may be explained by the increased mobility of white-tailed deer (and other *Odoicoileus* species) which are known to respond to increased food availability with increased mobility within their territories and home ranges (Gillingham and Bunnell 1989; Hanley 1997; Waller and Alverson, 1997; Etzenhouser *et al,*. 1998; Vercauteren and Hygstrom 1998). An increased mobility both in time and space in response to increased food availabilities has been documented with other mammals (Ball *et al,*. 2000; LoGiudice and Ostfeld 2001). Nothing is known to this respect regarding the *Mazama* genus. An aletrenative hypothesis offers less support from previous studies because very little is known on the functional response of populations of tropical herbivores (deer in particular) to increases in food availability. Very basic parameters such as rate of population increase are still lacking for the *Mazama* genus and nothing is known if this deer are capable of population functional responses to increased food supply. However, this has been documented for deer in temperate environments (Clutton-Brock *et al.* 1982, Hanley 1997).

It seems that the amount of fruits found in the diet of deer during the year is independent of the availability of fruits found on the trees and on the ground. Lower consumption of fruits were found when availability is also lower, but higher consumptions occurred irrespective of availability (Figure 3.16). Deer are mobile animals that normally wander around their home ranges performing a series of feeding bouts during the day and night (Gillingham and Bunnell, 1989, Hanley 1997). This mobility brings flexibility into the deer diet by putting the animal into the option of selecting either areas of high food availability or areas of low availability, depending on other factors that might influence its ultimate fitness. For example, areas of high food availability can be linked with high predation risks, pushing the animal to avoid this

areas and wander in longer or larger feeding bouts to fulfil their nutritional requirements. Areas of high food availability may lessen potential inter-specific comptetitive interactions. Conversely, areas of low food availability or where the availability is sparse over a large area, can be preferred if they provide other habitat needs (e. g. cover, protection, water, etc). Therefore it is not really surprising that the consumption of fruits by deer occurred more or less independently from other parameters such as temporal patterning of fruit availability.

However, it is important to remember that overall food availability was similar in the temporal patterns detected but differed in spatial patterns among the different forest types studied. The Lowland flooding forest presented a peak mean fruiting period during the dry season while the other habitats presented mean fruiting times during the wet season. This finding alone, can explain why the temporal occurrences in peaks of fruit consumption varied in the diet of deer by providing a third alternative hypothesis. Deer use habitats in relation with food availability, changing from one habitat to the next where their individual nutritional requests are best fulfilled. This has been widely documented in deer from temperate environments (Clutton-Brock *et al.*, 1982; Hanley 1997; Conrad *et al.*, 1999) and also in tropical environments (Aung *et al.*, 2001; MacShea *et al.*, 2001; MacCullough *et al.*, 2000).

It is concluded then, that the results found here on the spatial and temporal relationships of deer abundance, diet and food availability are more likely to be the result of deer using habitats in relation with food availability than from increased mobility of deer or as a result of population increases as functional responses.

The possibilities to extrapolate the results of this study to other areas, even within the GCR for deer management purposes are limited, because (i) the GCR exhibits a unique mosaic of vegetation associations that is more heterogeneous and diverse than previously thought (Martinez and Galindo-Leal, 2003) and therefore many of the patterns on deer diet, fruit phenology and availability and habitat characteristics are likely to exhibit considerable variations in habitats not included in the present study, (ii) deer are likely to adjust their diets and therefore use of plant resources according with changes in habitat heterogeneity that can influence food availability and (iii) deer management actions both for human utilization (e.g. hunting) or conservation, if they

are to be founded on ecologically sound decisions, should ideally utilize baseline information obtained *in situ* for the local population or meta-populations involved. The results of the present study can safely be considered as a general baseline information database to guide management decisions where the habitat characteristics are similar to those of the present study. This is represented by approximately 45% of the deer habitat of the GCR (around 50, 000 km^2) or 22% of the Southern Yucatan Peninsula in Mexico and Peten region in Guatemala and Belize (roughly 250,000 km^2).

CHAPTER FOUR

Spatial and temporal patterns of subsistence hunting of tropical deer populations

4.1. Introduction

4.1.1. Subsistence hunting

Wild animals have always been an important source of meat, skins and other essential goods for human populations (Fitzgibbon *et al*; 2000). At least one sixth of the total human population in the globe still has some links and forms of dependence from forest-harvested natural resources such as wildlife (Prescott-Allen and Prescott-Allen, 1982; Robinson and Bennett, 2000). Hunting for subsistence is still a common activity in many parts of the world, particularly in developing countries and remote areas such as the north-pole. Wild animals may contribute at least 20% and up to 70% of the protein requirements of people in at least 62 countries (Prescott-Allen and Prescott-Allen, 1982).

Caughley and Gunn (1996) define subsistence hunting as the "harvesting by an individual when the direct products of hunting are consumed or used by the hunters and their dependants". Commercial hunting (including the current "bush meat trade" crisis in Africa) is generally performed on a larger scale and its potential impact on wildlife populations is therefore greater (Robinson and Bennett, 2000, Fitzgibbon, 1998; Fa *et al*., 2002).

The effects and impacts of subsistence hunting in ecosystem structure and functioning have been studied just recently (Redford, 1992; Peres, 2000, 2001, Robinson and Bennett, 2000). The traditional idea of local and indigenous societies living in harmony with nature has been questioned and rejected during the past ten years with the overwhelming evidence of overharvesting coming from field research in Africa, Asia and Latin America (Alvard, 1995; Alvard and Kaplan, 1991; Robinson and Bennett, 2000). It is no longer believed that humans will harvest wildlife populations in a sustainable fashion when their individual or communal needs can be threatened or placed at risk by doing so (Redford, 1992, Alvard *et al*; 1996).

While both subsistence and commercial hunting is currently the focus of intensive field research in some central African countries to try to tackle the effects of the so called "bush meat crisis"; that might bring several species of apes and other wildlife to the brink of extinction (Fa *et al.*, 1995; Noss, 2000; Fitzgibbon *et al.*, 2000; Peres and Fa, 2002) the situation in Latin America is quite different. Subsistence hunting in Latin America has been the focus of research for at least a couple of decades but never with the intensity and preoccupation that the African scenario has brought recently.

In frontier areas of colonization in Latin America, subsistence hunting is one of the most important human activities affecting wildlife populations (Bodmer *et al.*, 1994, 1997). Frontier regions can sustain a large proportion of the global biodiversity and, paradoxically, are usually located in areas where human populations are characterized by extreme poverty and high population growth (Bodmer 1995a; Alvard *et al.*, 1996; Ericson, 1996). Subsistence and commercial hunting can clearly overexploit wildlife populations in these regions (Bodmer *et al.*, 1994). For example, conservative estimates of game yields indicate that as many as 23.5 million game vertebrates (equivalent to 84,224 tons of bush meat) are consumed each year by the rural population of the Brazilian Amazon (Peres, 2000)

Different animals are used by subsistence hunters in the neotropics but ungulates are by far the most important meat providers for local people (Robinson and Redford 1991; Bodmer *et al.*, 1994, 1995 a, b; Peres,1996; Cullen *et al.*, 2000; Jerozolimski and Peres, 2003). Among ungulates, peccaries, tapir and deer are top of the list as one of the most sought-after by subsistence hunters (Leopold, 1977; Robinson and Redford, 1991; Bodmer *et al.*, 1994; Clayton and Millner-Gulland, 1997; Peres, 2000; Hurtado-Gonzalez and Bodmer, 2004).

Studies on subsistence hunting in the neotropics suggest that compared with other ungulate species, deer can withstand considerable levels of hunting pressure, without an apparent effect on population size (Bodmer *et al*, 1994, Bodmer 1995a, 1997, Cullen *et al*, 2000, Robinson and Redford 1991). Deer resilience to hunting has been attributed to two main factors: their high reproductive rate and adaptability (Robinson and Redford 1991, Robinson and Bennett 1999, Robinson and Bodmer, 2000).

However, a recent study found that high levels of "poaching" by villagers in the vicinity of Barro Colorado National Monument, Panama were strongly correlated with low population densities of both white-tailed (*Odocoileus virginianus*) and brocket deer (*Mazama americana*) (Wright *et al.*, 2000).

4.1.2. The concept of hunting pressure from a landscape perspective

Several studies of hunting in the neotropics have documented how the abundance of wildlife differs between hunted, less heavily hunted and unhunted places (Hurtado-Gonzalez and Bodmer, 2003; Escamilla *et al.*, 2000; Carrillo *et al.*, 2000 among many others). These studies have used a variety of methods to obtain abundance and population density estimates in different areas, but none has ever provided a spatial estimation of hunting pressure.

Studies on the effects of subsistence hunting on vertebrate populations in neotropical forests have used the comparison between areas with and without hunting (Fragoso, 1991) areas with different "hunting pressures" and areas without hunting (Peres, 1990, 1996, 2000; Glanz, 1991) or between areas with "high" and "light hunting pressures" (Bodmer *et al.*, 1994; Bodmer, 1995; Cullen *et al.*, 2000).

The methods used for the characterization of "hunting pressure" are highly variable, ranging from the long term monitoring and recording of hunting yields (Silva and Sthral 1991, Bodmer *et al*, 1994, Bodmer 1995a, b. 1997) informal (semi-structured) interviews (Peres 2000) and structured interviews with hunters (Filion, 1981; Vickers, 1991), evidence of hunting encountered during field work (Fragoso 1991; Cullen *et al*; 2000) use of the opinion of Park guards or "experts" in the region (Wright 2000) or a combination of several of the above (Glanz 1991; Mittermeier, 1991; Peres, 1990, 1996, 2000).

While the best method to characterize hunting pressure is probably based either on the availability of hunting records or by the long-term monitoring of hunting yields, these methods are rarely used because hunting records in Latin America are usually lacking (Peres, 2000) and the monitoring of hunting yields can be extremely difficult and time consuming (Eves and Ruggiero, 2000; Bodmer, 1995). Moreover, some researchers

consider hunting pressure as a measure of human effort (e.g. man hours spent hunting) but this does not consider hunting success (Vickers, 1991).

Subsistence hunting is an extremely dynamic activity that leave few signs of its occurrence (Peres, 2000) and that can vary in intensity for several reasons. Hunting activities can be highly seasonal in some tropical regions such as the eastern Amazon basin (Vickers, 1991; Fitzgibbon *et al.*, 1995, 2000). Hunters can move considerable distances in search of prey (Mittermeier 1991) and can alter their prey preferences in response to prey availability (Vickers, 1991). Increased integration into the market economy encourages the sales of meat, thus blurring the distinction between commercial and subsistence hunting (Hart, 1978). Finally, it is possible that an area pre-conceived as having "light hunting pressure" based on interviews and field-hunting evidence may turn out to be heavily hunted (or vice verse) when assessed using appropriate hunting yield data or by acknowledging the spatial and temporal variations in hunting pressure (Filion, 1981, Marks, 1994). Moreover, all this information suggests that no unified concept exist to define the concept of hunting pressure and researchers have made use of it in different ways according to their particular needs.

Hunting pressure can therefore be a vague concept when the dynamics of both hunters and their prey are not considered in both time and space. It has been found, for example, that a heavily hunted area can be easily repopulated when refuge areas exist nearby or when the intensity of harvesting decreases in both time and space (Verkauteren and Hygstrom, 1998; Novaro *et al.*, 1999) and the behavioural responses of prey to space use by hunters can be adaptive and short-lived (Milspaugh *et al.*, 2000). Hunters return to preferred hunting sites (Thomas *et al.*, 1973) but when availability of prey decreases, hunters can rapidly move to find new catchment areas (Vickers, 1991). Therefore, if we are to understand the role of subsistence hunting in the ecology of tropical forest, while recognizing its importance for the millions of people that are heavily subsidized by this activity, it is imperative to better understand the concept of hunting pressure in many vertebrate groups, including deer.

Despite the importance of potential variations in time and space of the intensity of hunting of many wildlife populations (Fitzgibbon *et al*; 2000), no study of subsistence

hunting so far has ever measured the spatial and temporal allocation of hunters in the landscape. To date the only two studies that had made use of a landscape approach to address the effects of human hunting pressure on wildlife populations have been carried out in temperate environments (Lyon and Burcham, 1998; Broseth and Pedersen, 2000). Lyon and Burcham (1998) pioneered the use of GPS technology to track deer hunters and their activities in Colorado, but it was Broseth and Peddersen (2000) who first proposed the combined use of GIS/GPS technologies to better understand the effects of hunting intensity on wildlife populations.

4.1.3. The estimation of hunting catchment areas

Hunting catchment areas can be defined as the area of forest or other habitats used by hunters for which estimates of hunting pressure such as total harvest off-takes can be obtained (Robinson, 2000). Although several methods can potentially be utilised to estimate the spatial arrangement of hunters and their catchment areas, little use has been made of them because it is usually difficult to obtain information on the specific location where subsistence hunters perform their activities. Hart (2000) pioneered the use of the Minimum Convex Polygon (MCP) method to estimate catchments of indigenous hunters in Zaire, but he used hunting camps rather than actual killing locations for his estimations. This is probably the only published study of subsistence hunting that make use of this kind of methods.

In the MCP method (developed for home-range estimation) the outermost set of data points representing a number of locations (e.g. an animal's locations or GPS positions) are connected to form a polygon with no concave sides. Developed before the advent of computer digitisation, it is easy to implement graphically, although it suffers from a number of disadvantages, such as a tendency to overestimate home-range (in this case catchment) sizes (White and Garrott, 1990). However, the MCP has been widely used and is a useful method for comparative purposes with previous studies.

Of the several methods available other than the commonly used MCP, the calculation of harmonic mean polygons and the probabilistic kernels are among the most popular (White and Garrot, 1990).The harmonic mean calculates harmonic-mean values at grid points systematically overlaid on an animal's area of use (Dixon and Chapman, 1980), but it has many drawbacks. It does not produce a probability density function,

and hence it is difficult to interpret; it is sensitive to the size of the grid arbitrarily chosen by the user; it produces misleading results when data points occur near grid-line intersections; and it has been shown to be an inappropriate application of kernel methods (Worton 1987, 1989a).

There are two main variants of the probabilistic Kernel method: the Fixed Kernel (FK) and the Adaptive (or variable) Kernel (AK). In the FK method, a single smoothing width is used on all the observations in the sample. In the AK method, local adjustments are applied to the width of individual kernels. Observations in areas of high density get less smoothing (tighter fit), and observations in areas of low density get more smoothing (looser fit) (Worton, 1989a). Although the AK was expected to produce better results, the FK generally produces estimates of home-range size and contours with lower bias than the AK in simulation studies (Worton, 1995, Seaman and Powell 1996). The AK however, gives the advantage of selecting probabilistic values for the kernels (isopleths) according with the smoothing width (variance) present on the sample (Worton, 1995).

The AK is a non-parametric estimation procedure that is applicable to a variety of home-range (in this case catchments) estimation problems where the assumptions of a parametric model such as the bivariate normal cannot be met (Worton, 1989b, 1995). The AK is free of the problems associated with the harmonic mean and MCP. The AK technique can produce a probability density estimate of a distribution based on a sample of points for data of any number of dimensions. The probability density estimate that is produced by kernel methods may be directly interpreted as a utilization distribution (UD) (Van Winkle, 1975). Worton (1989) introduced AK as home-range estimators. The use of Kernels for the estimation of animal abundance was first proposed by Seber (1986). AK have several desirable qualities for density and home-range estimation: (1) they are nonparametric, and therefore have the potential to accurately estimate densities of any shape, provided that the level of smoothing is selected appropriately; (2) they produce a density estimate directly; and (3) they are not influenced by grid size or placement (Silverman 1986). Worton (1987) reviewed home-range estimators, including AK. Worton (1995) and Seaman and Powell (1996) evaluated the accuracy of AK for home-range estimation.

AK use statistical techniques for estimating the density of a distribution at any point. The density estimate is derived from the proximity of observations (sample points) to each evaluation point. Evaluation points may be the observations themselves, or a regular grid laid over the sample. The methods are described in more detail by Worton (1989a, b), and Seaman and Powell (1996). The methods impose a kernel over each observation. A familiar example of a kernel is the normal distribution, though kernels of other shapes exist and are often preferred over the normal for computational speed. The estimate of the density at any given evaluation point is essentially the average height of the kernels that overlap the evaluation point (Wray *et al*; 1992).

The width (variance) of the Kernels affects how much smoothing occurs and is referred to as the bandwidth, smoothing width, or smoothing parameter "h". Kernel estimates are highly sensitive to the bandwidth; thus, to get accurate results it is crucial to correctly select the value for this parameter (Worton, 1995; Seaman and Powell, 1996).

A significant difficulty with AK is their high sensitivity to the variance. For many datasets, using a Least Square Validation (LSV) to select the smoothing variance produces good results. However, LSV does not work acceptably for datasets with multiple observations at identical locations (e.g., trap grid data, animals in dens or nests; Silverman 1986). As long as the locations are different (e.g. radio-telemetry data, GPS localization) LSV produces excellent results (Seaman and Powel 1996).

Mack and Quang (1998) introduced the use of AK for estimation of population density based on distance data in line and point transect sampling. They conclude that the Kernel approach is a viable alternative to other existing estimators because it does not require specifying a horizon, a severe shortcoming in the Fourier series method. The confidence intervals of the density estimations with this technique can latter be corrected for biases (Mack, 2002).

The potential applications of kernel methods for estimating hunting pressure from a temporal and spatial perspective are therefore enormous. If specific information on where, when and how much is being hunted in a given landscape is possible to obtain; then kernel methods can be used to predict with a high degree of probability and

statistical confidence, the extent and reach of specific levels of hunting pressure in that landscape.

4.2. Chapter aims

The spatial analysis of deer hunting patterns has been studied to some extent in temperate environments, but remains poorly known for tropical environments. So far, there are no spatially-explicit studies in the literature that document, how hunters move, when they do it and for what reasons when harvesting deer (and other wildlife) in the tropics. Little is known on how people make use of the space when harvesting wildlife in tropical forests and what the effect of this space use can be on animal populations and communities (e.g. when several sympatric species co-exist). Moreover, the number of deer species endangered from over-harvesting in Latin America and elsewhere (Wemmer, 1998; Weber and Gonzalez, 2003) make this kind of knowledge a high priority to be able to establish conservation and management actions.

This chapter aims to describe the spatial and temporal patterns of deer hunters in a tropical forest landscape and provide an alternative approach to model and predict the effects of hunting pressure on sympatric populations of the red brocket deer (*Mazama americana*), Yucatan brown brocket deer (*Mazama pandora*) and white-tailed deer (*Odocoileus virginianus*) in the tropical forest of the Greater Calakmul Region, Campeche, Mexico.

The modelling approach makes use of extensive GPS locations of deer hunting kills interspersed in space and time in a large study area (155,000 ha) representative of the Greater Calakmul Region. The first approach uses the common Minimum Convex Polygon technique (MCP) to calculate hunting catchment areas. The second, makes use of a conventional radio-telemetry technique (the Adaptive Kernel method) to obtain spatial probabilistic representations of both, hunting pressure and deer abundance indices. Finally, an attempt was made to estimate sustainable harvest rates for the three species of deer using both the Robinson and Redford (1991) "production" model and the Bodmer (2001) "harvest model" as well as proposing maximum deer harvest quotas (for management purposes) using the spatial and temporal information on deer harvest and catchment areas obtained in this study for a source-sink model.

The chapter make use of information generated in previous chapters, such as aspects on deer abundance and habitat use (Chapter 2) population age and sex structure (Chapter 2) and deer habitat characteristics, such as major vegetation associations and topography (Chapter 3) The results are discussed on the light of other similar studies for deer in temperate ecosystems and for other species in the tropics. The main conceptual frameworks in this chapter were the theory of central place foraging (Stephens and Krebs, 1986) for discussing the space use of hunters and the niche theory (Pulliam 2000) and sink/source theory (Pulliam 1988) for analysing the potential effects of hunting on deer populations.

Additionally, I tested the hypothesis that hunting records are not different from sighting records in its spatial location by deer categories and different cohorts in an attempt to validate its use for other modelling approaches (see Chapter 5). A series of statistical comparisons on the spatial location of both hunting and sighting GPS records was performed to test this secondary hypothesis.

4.2. Methods

4.2.1. Spatial GPS data collection

From February 1996 to August 1999 and then again from March to December 2001, spatial information on deer hunting was collected in the Nuevo Becal community and study area (see Chapter 1). Hunters were asked to participate in the study by providing information on their deer hunting outings, success and location. One hunter was hired as a field assistant during this period and trained in different tasks necessary for the development of the project. He was trained in data collection and recording in a field diary, map reading and interpretation, GPS use, deer skull and mandibles preparation and deer sex and age estimation. This person collected some of the spatial data presented in this chapter when I was not able to do so myself.

For the spatial analysis of deer hunting it was particularly important to record with a GPS the approximate location (as accurate as possible) of individual deer killing points by participating hunters (including the field assistance himself that happened to be one of the top hunters in the community). For this, we accompanied the hunters to the killing sites either on the day of the hunt or an average of one week after the deer hunt had happened. For a few remote points, the location was marked by the hunter and the exact coordinates where later recorded during a second trip, sometimes several months after the hunt had taken place. For each site, the following information was collected:

1. GPS location.
2. General location data: date, forest canopy closure (therefore, approximated GPS precision), number of satellites on signal and approximate error from the marked point (e. g. distance away to improve satellite reception).
3. Hunter data: Name, age, date of hunting, transportation to hunt.
4. Deer information: species, sex, age and data of specimens collected (skull, stomach contents, tissue reference numbers)
5. Habitat data: Vegetation type, distance to roads, distance to town

For practical reasons, "killing" points (the point where the animal was actually shot) and "retrieving" points (the point where the deer carcass was actually recovered after the shot) are considered the same and used interchangeably here, because there was some variation in the identification and location of both points. In most *Mazama* sp

cases when the hunter was hunting solo and with a large calibre shotgun (20 gauge or bigger), the killing and retrieving points were actually the same. When the hunting involved the larger white-tailed deer, the use of dogs and/or the use of small calibre weapons (.22 caliber rifles) the killing point could be as far as one kilometre away from the actual retrieving point. When this happened (in very few cases, n = 5 from 60 total GPS records used) most hunters were unable to locate the original "killing" point and therefore the retrieving point was recorded. Some white-tailed deer "killing" points were actually recorded as "retrieving" points, because some evidence (e. g. blood stains, deer hair, smashed vegetation, carcass remains or rubbish left by the hunter) was found in some cases or because the hunter was unable to remember the exact location of the shoot.

For each GPS killing location an average error of 100 meters radius was estimated from the exact deer killing (or carcass retrieving) point based in two assumptions: (1) Under very closed forest canopies, the GPS reception was poor (an average of 2 satellites contacted for reception) and the exact location has to be moved an average of 100 meters to a point with an open canopy where satellite reception improved to at least four satellites. When a clear canopy gap was impossible to find, either the climbing of a large tree or (in a few extreme cases) the clearing of vegetation to form a "canopy gap" for improved satellite reception was performed in the closest location to the actual killing point. (2) Based on a number of points where the hunter responsible of the killing was unable to find the exact location of the killing/retrieving point and that a latter thorough search found it, within an estimated 100 meters error distance from the original point estimated by the hunter.

GPS coordinates were obtained using a Trimble II Geo-Explorer hand-held GPS receiver (Trimble Inc., Palo Alto, California) for most of the work carried out from 1996-1999 and later a Garmin e-Trex GPS, (Garmin Corp. Olathe, Kansas) during 2001. Both units have similar accuracies of around 3 to 5 meters (even under heavy canopy cover) when satellite reception was at least from four satellites and for non differentially-corrected data. No attempt was made to perform differential correction of the GPS data given the margin of error inherent to the collection of hunting records.

Deer hunters in the study area use basically three methods to kill deer. By far the most common method is "stalking". In this method, hunters engage into finding deer fresh signs and then stalk the animals alone and in silence in search of an opportunity for a short distance shot. Dogs are sometimes used but normally left in base camps and used to retrieve wounded animals. Hunters normally stalk alone or in pairs walking slowly and in silence throughout the forest. A slight variation of this method consist of stalking at night with the help of head-lamps. Hunting alone is mandatory in this cases because absolute silence is paramount to achieve hunting success. A second method consists of the use of dogs with which they pursuit deer (usually in parties composed of three or more hunters) and several dogs. Deer are "shot on the fly", that is; when passing animals run fast with the dogs close-by in pursuit. This method is sometimes used during the dry season when stalking is difficult because of the noise produced while walking on the accumulated dry forest debris. Finally, a very uncommon method in the GCR consist of finding a deer-favourite fruiting tree in fruit bloom or an isolated "aguada" (water pond) visited by wildlife during the peak of the dry season. Then the hunter sit and wait for the deer (or other wildlife) to come. Some hunters occasionally hang hammocks on the top branches of these trees and wait for a night shot with the help of a head-lamp.

Although hunters use all this methods to kill deer in the GCR, the prevailing method for deer hunting by the hunters surveyed in this study in Nuevo Becal was stalking alone or in pairs. Dogs were used, but only to retrieve killed or wounded animals, although in a few cases hunters also used dogs to chase and pursuit brocket and sometimes even white-tailed deer. Based on the interviews, an attempt was made to differentiate the different methods used to stalk and hunt deer and to evaluate their influence in the spatial patterns reported. However, because most deer hunting was performed by hunters stalking alone no differences in hunting methods are considered for the spatial and temporal analysis of hunting.

Most hunters walk to their preferred hunting grounds or use bicycles. A few of them own light motorbikes and use them extensively for their hunting expeditions when their catchment areas are farther away than 5 kilometres from the village and even fewer own horses as a mean of transport. Only the few major dust roads are used for vehicle (either bicycle or motorbike) or horse-back riding transport and most hunting

is performed while walking in secondary logging roads or throughout the forest. No hunter surveyed during the study period owned a car and only two or three old pick-up trucks belonging to wealthy members of the community (that do not normally engage in hunting activities) were detected from 1996 to 2001. This situation, however; is rapidly changing as more and more members of the Nuevo Becal ejido are getting economically more fluent and access to motorbikes and cars are currently more common.

More or less once a month, the households of participating hunters were visited to provide presents (usually food items or clothes) for their cooperation in the study and these visits were used for gathering extra information such as non-recorded hunting outings and hunting success and information for other than the targeted species of deer. Using the information retrieved from these interviews, a 10% additional data on either missing successful deer hunting expeditions or missing GPS locations was estimated as an average for all participating hunters.

4.2.2. Hunting vs. sighting data

To test the hypothesis that both hunting records and sighting records (recorded during transect surveys, see Chapter 2 and opportunistically during other visits to the forest) are no different in its spatial arrangement and therefore can be used to estimate some hunting parameters, deer sightings (either in transect surveys or opportunistic observations) were added to the data base, when the exact GPS location, deer species, sex and age class (adult, juvenile) were recorded. To test this hypothesis, one-way ANOVA tests (after Kolmogorov-Smirnoff and Levene's test for normality and homogeneity of variances, respectively) were performed for habitat type, distances to town, distances to road and distance from agriculture and second growth vegetation (thereafter all deforested areas). When these assumptions were not fulfilled, then their equivalent non-parametric test was used (Kruskal-Wallis test, Wilcoxon's test or Log likely-hood G test for paired data).However, hunting and sighting data were not used indiscriminately; only hunting data was used for the calculation of harvest rates and catchment areas.

4.2.3. Hunting distances to town

To calculate the distances to the deer killing points to the main human settlement (town), the minimum straight distance from the GPS points to the centre of the village was calculated using the extension Distcalc v.3.1 for ArcView 3.2 (Jenness 2004). The approximate centre of the village (downtown square and sports areas) to the centroid of the record was used for all measurements. All of the participating hunters (with one exception) live in this main cluster of house-holds around the centre.

Buffers of the mean and upper and lower confidence intervals of the variable "distance of deer hunting to village" were created for all villages in both the study area and for the Grater Calakmul Region. All human settlements larger than 250 inhabitants (as for 1997 INEGI official Land Use/Land tenure maps) were selected and overlayed with the land tenure and Calakmul Biosphere Reserve polygons (Garcia and March 2001) and vegetation classification map (modified from Martinez and Galindo-Leal 2003 but see Chapter 2) for a spatial extrapolation of the potential extent of deer hunting pressure in the region using this parameter.

4.2.4. Hunting distance to roads

The closest distance to roads was calculated with the extension Nearest Features v.3.7 for ArcView 3.2 (Jenness, 2004) using the deer kill record weighted mean centoid as the measuring point. In conjunction, these program automatically select the nearest point on the road to the centroid of the record. Only major dust roads were used for this calculation and the statistical analysis. However, the distance of points to secondary roads such as mapped logging roads and trails was also calculated and mapped but no attempt to perform statistical analysis was done because it was not known if the hunter actually used this roads or followed a different paths throughout the forest to hunt. The estimated "alternative route" from the nearest major road to the hunting point was estimated instead using the extension Alternate Animal Movements v2.1 for ArcView 3.2 (Jenness, 2004). This extension uses the elevation and slope map grids of the study area to calculate the alternate "flattest, shortest and therefore easiest" alternate route between two locations, that can be either both point features or one point and one line feature (Jenness, 2004). The shortest distance to road and the

alternate "flattest, shortest and therefore easiest" routes can then be spatially compared.

4.2.5. Catchments areas obtained with MCP

Catchment areas by hunters, seasons (dry, wet), years and deer species were calculated using the Minimum Convex Polygon (MCP) of deer kill GPS locations. The Animal Movement v 2.1 extension (Hooge and Eichenlaub, 1997) was used for this calculations within ArcView 3.2. Finally, to assess the effects of habitat differences on the spatial hunting patterns, the minimum distance of each deer kill centroid to the nearest vegetation type was measured using the Distance and Bearings between Matched Features (DBMF) extension v. 1.4 (Jenness, 2004).

4.2.6. Catchment areas obtained with Adaptive Kernel isophlets

A second method to estimate catchment areas was used by calculating the Adaptive Kernel isopleths (AK) of the density of GPS deer killing locations. To obtain the kernels a 99% probability (one confidence interval (CI) was set for high hunting pressure at >5 deer/km^2; 98% probability (2 CI) for moderate hunting pressure at between 2 and 4 deer/km^2 and 95% probability (5 CI) for low hunting pressure at <1 deer/km^2 (Mack 2000, Mack and Quang 1998).

Kernel polygons were obtained for the each year of deer harvest, the three species of deer, all juvenile, all adults, all males, all female deer and finally for all deer pooled together to produce a general hunting pressure map. The final overall hunting pressure map was cross validated using the Least Square Validation method (Worton, 1989a, b; Hooge and Eichenlaub, 1997) to obtain a final validated probabilistic map of the spatial arrangement of hunting intensity by harvest rates. The AK and its statistics (Least Square Validation) were calculated using the program Animal Movement v 2.1 extension for ArcView 3.2 (Hooge and Eichenlaub, 1997).

This technique extrapolates the commonly used method in radio-telemetry studies for assessing the home-range of animals based on both the distribution and density of spatial locations to predict probabilistic contours of occurrence (Worton, 1989a). In this case, the probability of having deer hunted at a given rate per surface unit of terrain was used as the main predictor variable. Thus, the kernels reflect the

probability of having deer killed at any given rate per square kilometre. Only deer hunting GPS records of the cooperating hunters were used for the calculation of hunting catchment areas and harvest rates.

4.2.7. Deer harvest rates and proportional area hunted.

Harvest rates were calculated by dividing the number of deer killed per polygon area obtained either with the MCP or AK techniques. The total harvest rate was calculated by dividing the total number of deer killed between the surface of the study area.The proportion of the area hunted was calculated by dividing the respective surface catchment area between the surface of the study area. Harvest rates are reported as deer/km^2/year

To estimate "sustainable harvest rates" of deer hunting, the widely used Robinson and Redford (1991) "production model" and the Bodmer (2001) "harvest model" were used. Robinson and Redford's (1991) production model assumes that theoretical estimations of maximum production rates (n animals produced/km^2/year) are compared to actual harvest rates (n animals harvested/km^2/year). This model is particularly useful in the absence of data of absolute densities and actual production rates and is used for detecting possible over-harvest but cannot detect sustainable hunting (Robinson and Bodmer 1999). The main limitations of this model are that P_{max} (maximum production) rely on approximations rather than on actual figures on intrinsic rate of increase (r). Bodmer's (1991) "harvest model" uses calculations of actual population density, reproductive productivity (again an approximation of P_{max} given the lack of reproductive information on deer in the study area) and harvest rates of hunted populations. This model can be used to assess whether hunting is sustainable or not (Robinson and Bodmer 1999). Both models assume that production (P_{max}), maximum potential harvest (MH_{max}) and growth rates (r_{max}) of wildlife populations are density dependent. Likewise, both models assume that Maximum Sustainable Yield (MSY); defined as the maximum possible number of animals harvested without driving the population into decline (Caughley 1978) should be about 0.6 of the carrying capacity (**K**) in species with relatively high reproductive productivity such as deer (Robinson and Redford, 1991; Robinson and Bodmer 1999, Bodmer, 2001). Given the lack of reproductive data for deer in the GCR, productivity

data was obtained from the literature (Hurtado-Gonzalez and Bodmer, 2004) for the calculation of the models.

For local management purposes, an attempt was made to calculate what I call "Maximum Annual Harvests" (hereafter MAH) of deer, using the annualised information from the spatial arrangement of hunting and the harvest rates per catchment areas obtained from 1996 to 1999 as calculated with the Kernel probabilistic method. MAH was conservatively defined as the number of animals taken per square kilometre per year when hunting pressure was considered "moderate" so that a likely "source-sink" dynamics persisted over the years. A "source" area was defined as an area where hunters harvested deer at low to moderate hunting pressures (< 2 deer/km^2/year) for one year and then moved to a different catchment area for the next year. The number of adult deer harvested in "source" areas must be larger than that of juvenile assuming a low mortality rate, high reproduction turnover and emigration of juveniles. A "sink" area was defined as that where hunters harvested deer at high hunting pressures (> 3 deer/km^2/year) and persistently hunted this area through the study period (1996-2001). The number of juvenile deer harvested in "sink" areas must be larger than that of adult deer therefore assuming a high mortality, low reproduction and constant immigration rates. Therefore, two different MAH rates were calculated: one for the hypothetical "sources" areas and another one for the "sink" areas.

4.2.8. Estimating spatial indices of hunting pressure

Hunting pressure was therefore assessed by three independently obtained methods: (1) the harvest rates (number of deer killed per square kilometre per year) within catchment areas obtained with the MCP technique, (2) harvest rates obtained with probabilistic AK isophlets (AK) of hunting intensity and (3) using the mean distance of deer hunting to village (+/- one 95% confidence interval) to "buffer" the probable extent of deer hunting from all the villages within the study area and the GCR. Hunting pressure was rated as "high" when the harvest was > 3 deer/km^2, moderate when it was between 1-3 deer/km^2 and low when < 1 deer/km^2. Hunting pressure was not rated when distances to villages were used to estimated the potential extent and reach of deer hunting.

4.2.9. Estimating the extent of deer hunting pressure within the villages

The spatial and temporal information on hunting came from a sample of hunters within one village (Nuevo Becal) willing to fully participate in this long-term research project from 1996 to 2001. Other hunters were unwilling to participate but accepted to be interviewed in order to assess their deer hunting intensity, success and catchments within their communities.

Interviews (both structured and informal) were used to assess the number of hunters in both the main human settlement where this research took place (Nuevo Becal) and in the other 4 major local communities within the study area and immediately adjacent to the Nuevo Becal land-hold: Alvaro Obregon (Zoh-Lahuna), Nueva Vida, El Refugio and La Mancolona. Meetings with the administrative heads of these communities allowed to assess the total number of households, families and men of working ages. Later, meetings and interviews during the traditional "last-Sunday-of-the-month" gatherings in each community permitted the estimation of the number of active hunters, their prey preferences, locations for hunting and hunting intensity. Additionally, field notes of the encounter of individuals in hunting activities while performing other field research where used to corroborate the accuracy of the information obtained from interviews.

This qualitative and quantitative information allowed for the calculation of the proportion of hunters willing and unwilling to participate in the study, as well as their hunting whereabouts, hunting intensity and likely contribution to the overall deer hunting pressure in the study area. However, no attempt was made to use this information in a similar fashion to that obtained from the participating hunters (e.g. calculation of catchment areas or harvest rates) but merely as an indication of general, human community-wide deer hunting patterns in the study area.

4.2.10. Estimation of spatial abundance indices.

For the estimation of deer abundance spatial indices that are comparable with the catchments areas and spatial hunting pressure assessments obtained, the following method was developed:

The information on deer abundance comes from the 23 non-permanent transects were deer abundance was estimated with the count of deer sign encounter rates (SER) from

March 2001 to February 2002 (Figure 2.1, Chapter 2). During the monitoring of these transects, sections of 100 meters were marked with flagging tape and therefore a rough estimate of the exact location of each individual detection event can be positioned within the length of the transect at 100 meters intervals. Only the transects (n = 21) with no overlapping sampling areas were chosen for this analysis.

To accomplish this, the following four steps are necessary: (1) The exact GPS location of the transect and its total length was incorporated into a GIS line coverage. The habitat gradients that the transect crosses can be estimated by overlaying the transect with the vegetation map of the study area. (2) The approximated location of deer SER detections events is digitalized as a point coverage, overlaying the transect coverage using the information on transect length and the 100 meters sections in order

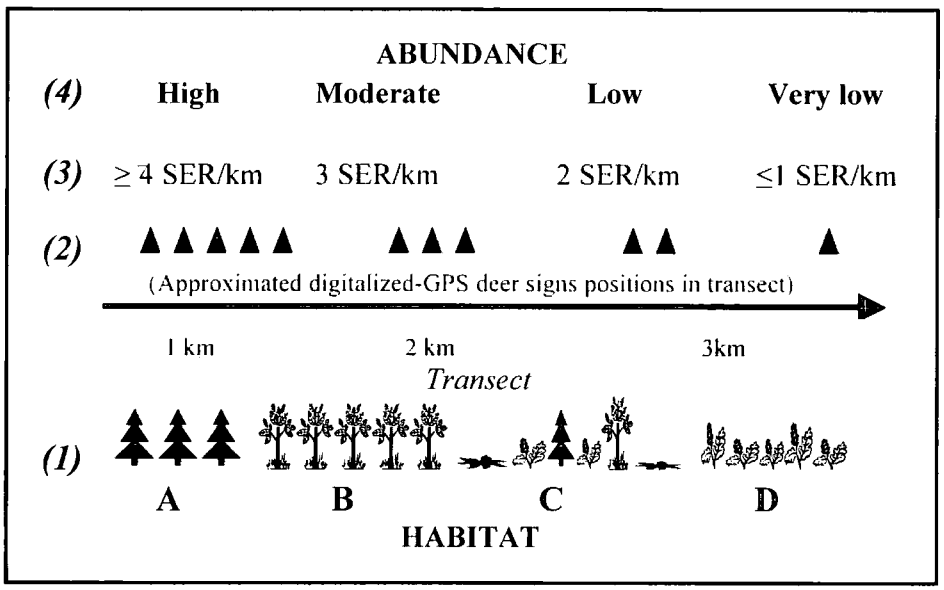

Figure 4.1. Schematic representation of the method used to create spatial deer abundance indices with the help of the GIS and deer sign encounter rate data. More information on how SER data was obtained can be found in Chapter 2.

to pinpoint the exact location of the detection events. (3) Because the amount and spatial distribution of detection events can be extremely variable within the transects in absolute numbers, a rating system of SER location is used rather than exact numbers. This rating system uses the following categories to group SER events into point clusters: ≤ 1 deer signs/km = 1 point; between 1 to 2 deer signs/km = 2 points; between 2 to 3 deer signs/km = 3 points and ≥ 4 deer signs/km = 4 points. (4) This

rates are considered equivalent to very low, low, moderate and high abundance of deer signs, respectively and therefore can be interpreted as an spatial index of relative abundance, where probabilistic Kernel isophlets can also be estimated using clustered deer sign groups rather than number of signs. It is argued that this method provides an accurate picture of deer abundance at the landscape level when mapped with the AK method (Figure 4.1).

For this analysis all SER from both *Mazama* spp. And *Odocoileus virginianus* were pooled, therefore when referring to "deer" is meant to be the three species present in the study area. To calculate AK with this information, the same procedure used to calculate AK for deer cathment areas can be followed. High deer abundance was estimated with a 95% probability or 1 confidence interval (CI) that $\geq$ 5 SER/km will occur; moderate deer abundance with a 90% probability or 2 CI for 2 to 3 SER/km; low deer abundance with 85% probability or 3 CI for 2 SER/km and very low deer abundance with an 80% probability or 5 CI for $\leq$ 1 SER/km. Finally, a least-square validation of the Kernel isophlets is performed and the map can now be compared with the other maps calculated for hunting catchment areas. The AK provide a spatial representation of the probability of finding a given deer sign encounter rate per square kilometre (SER/km^2) in a landscape sampled with systematic, random, stratified transects. This might be interpreted as an indirect method for the spatial representation of the relative abundance of deer in that sampled landscape. All GIS extensions used are freely available for download through the internet and require ArcView 3.x with Spatial Analyst extension installed on a Microsoft environment.

4.2.11. Statistical Analysis

A test for normality (Kolmogorov-Smirnoff test) and homogeneity of variances (Levene's test) were applied for all data sets and then either one-way ANOVAS or one-tailed t-tests (when normality and homogeneity of variances assumptions were fulfilled) or its non parametric equivalent (e. g. Kruskal-Wallis test, Log likely-hood or Wilcoxon tests) were selected accordingly. All statistical tests were performed using SPSS version. 10 and/or SpaceStats version 2.1 for Windows software, after Zar (1989).

4.3. Results

4.3.1. Hunting versus sighting data

A total of 60 deer hunting records and 32 sighting records with complete information of deer species, sex, age and temporal and spatial hunting data were incorporated into the GIS data base (Figure 4.1). Deer hunting data was collected for a period of four uninterrupted years (1996-1999) with the full of cooperation of nine hunters for which a 10% error in missing hunting information was estimated with the use of regular interviews. Deer sighting data was collected for a period of five interrupted years (1996-99 and 2001) (but see Chapter 2).

There were no differences in the number of adults and juvenile deer harvested (G test = 9.4, d. f. = 1, $p > 0.5$) but there were significantly more adult deer sighted than juveniles (G test = 32.4, d. f. = 1, $p < 0.05$) (Figure 4.2).

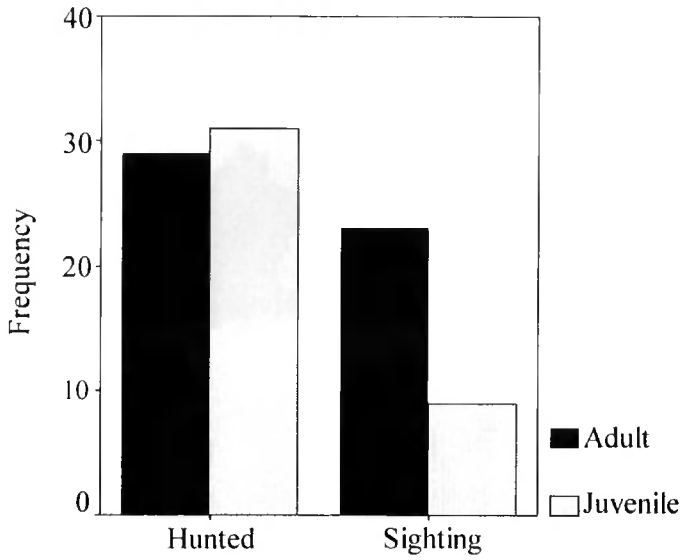

Figure 4.2. Proportion of adult and juvenile deer in hunting and sighting records in the study area within the GCR, Mexico.

The proportion of both *Mazama* species were similar between hunting and sighting data, but there were considerably less white-tailed deer sighted than hunted (Figure 4.3). This is congruent with the general trends in the abundance and population density of this species of deer in the GCR (Chapter 2). However, the proportion of both sighting and hunting records during the dry and wet seasons is similar and no statistical differences were found in the seasonality of frequencies of both kind of records. (Figure 4.4).

The proportions of species hunted and sighted was also different (Figure 4.3).This difference was statistically significant (G test, 14.7, d. f. = 2, p <0.05) and therefore no attempt was made to use both sets of data to test for spatial differences among different species of deer.

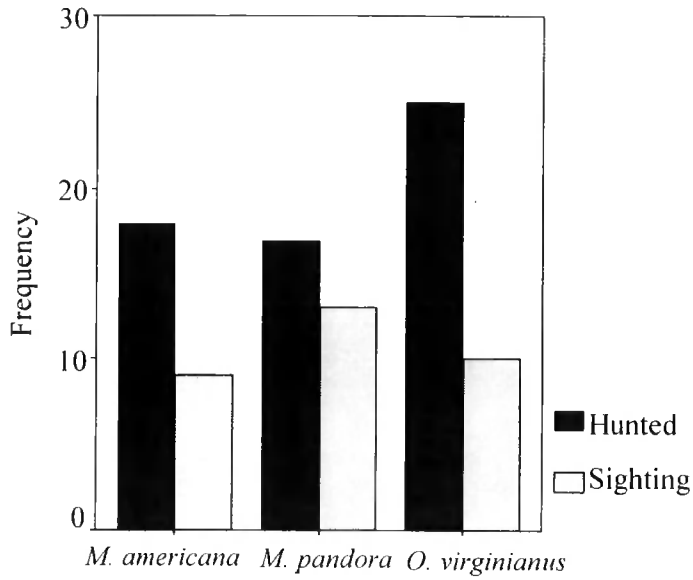

Figure 4.3. Proportions of the three species of deer (*Mazama americana*, *Mazama pandora* and *O. virginuanus*) hunted and sighted in the GCR Campeche, Mexico.

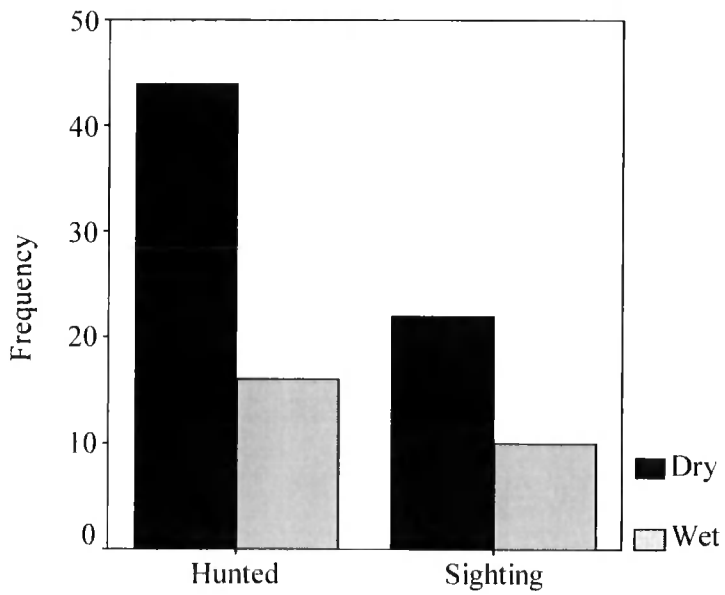

Figure 4.4. Proportion of deer hunting and sighting records during the dry and wet seasons in the study area within the GCR, Mexico.

The same is true for the proportion of males and females observed and hunted, but no statistical test can be performed due to small sample sizes in sighting records (Figure 4.5). This bias and differences were likely caused by the difficulty in accurately aging and sexing deer through visual observations in the wild, that can be extremely difficult in the study area.

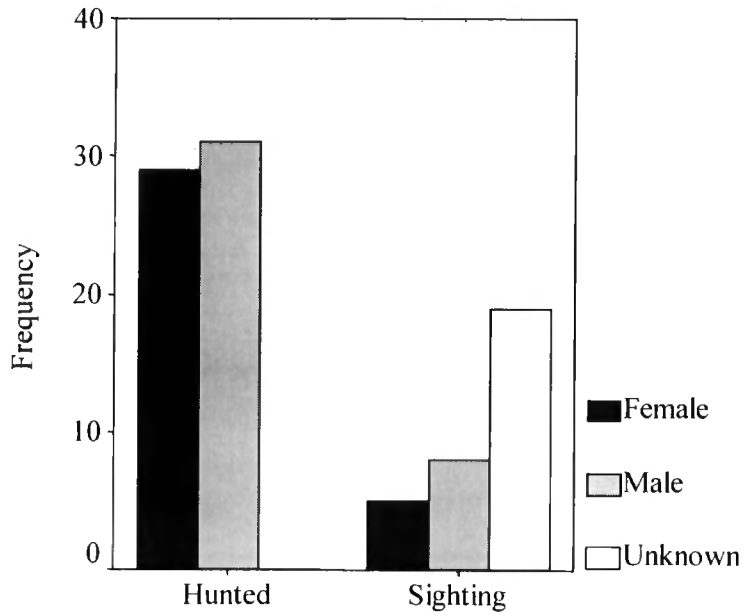

Figure 4.5. Proportion of sexes between hunting and sighting records in the study area within the GCR, Mexico.

Finally, the proportions of adults and juvenile deer in both sighting and hunting records was equivalent and no statistical differences were found (G test = 1.01, d. f = 2, $p > 0.05$) (Figure 4.6).

This preliminary analysis of hunting and sighting data was necessary to find out which data is comparable and can be used without biases for the estimation of other parameters. The results suggests that major differences exist in all but the proportion of ages (juvenile and adult deer).

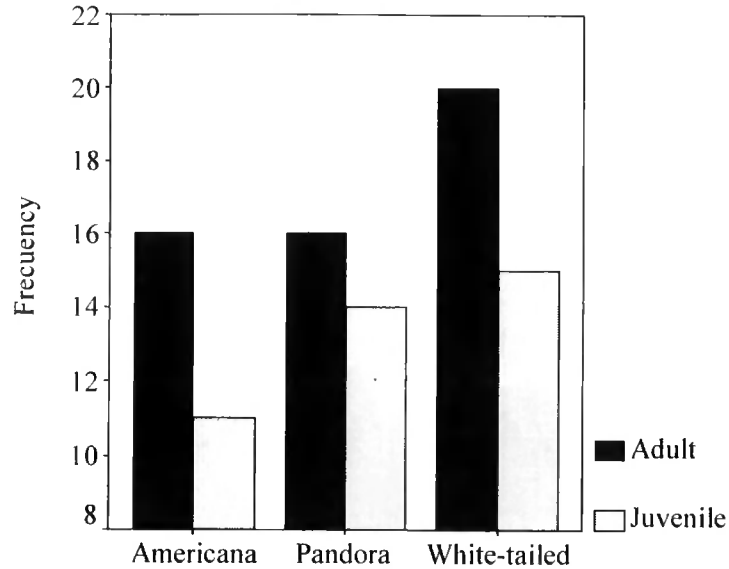

Figure 4.6. Proportion of juvenile and adult deer in both hunting and sighting records in the study area within the GCR, Mexico.

4.3.2. Hunting distances to town

Differences in the mean distance to town were not detected between hunting and sighting data (ANOVA f = 1.348, d. f. = 2, p> 0.05) (Figure 4.7).

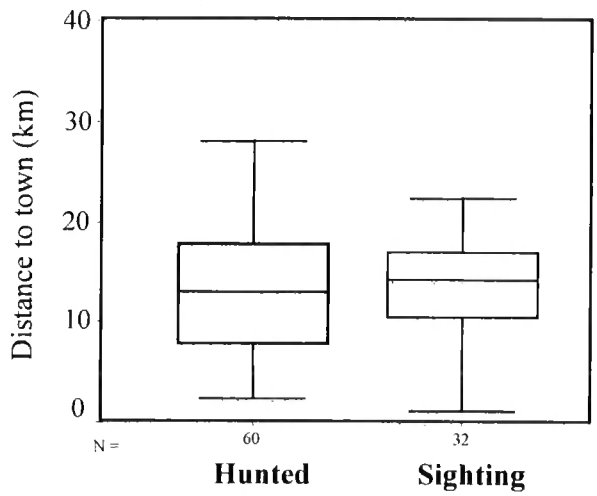

Figure 4.7. Mean and one confidence interval of distance to town between hunted and sighted records of deer in the GCR, Campeche, Mexico.

The mean distances of hunting to town were significantly different among deer species (ANOVA f = 3.688, df = 2, p < 0.05), ages (ANOVA f = 5.91, df = 1, p < 0.01) and seasons, but not between sexes (ANOVA f = 0.685, df = 2, p > 0.5) (Figure 4.8, Table 4.1). However, the total number of adult and juvenile deer recorded by both

sightings and hunting was not statistically different between species of deer (Kruskall-Wallis test, $x^2 = 0.231$, df = 1, p>0.5).

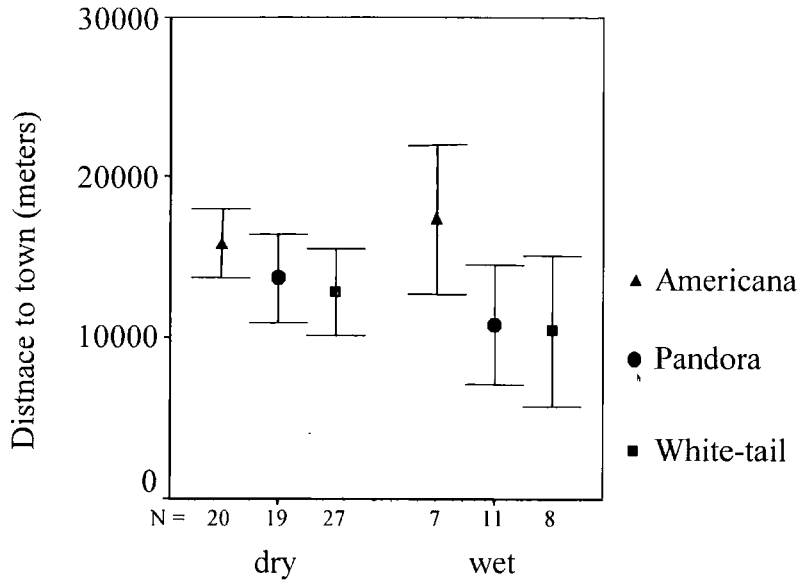

Figure 4.8. Mean and one confidence interval of distance to town between the three species of deer in the GCR, Campeche, Mexico (both hunted and sighting data are presented).

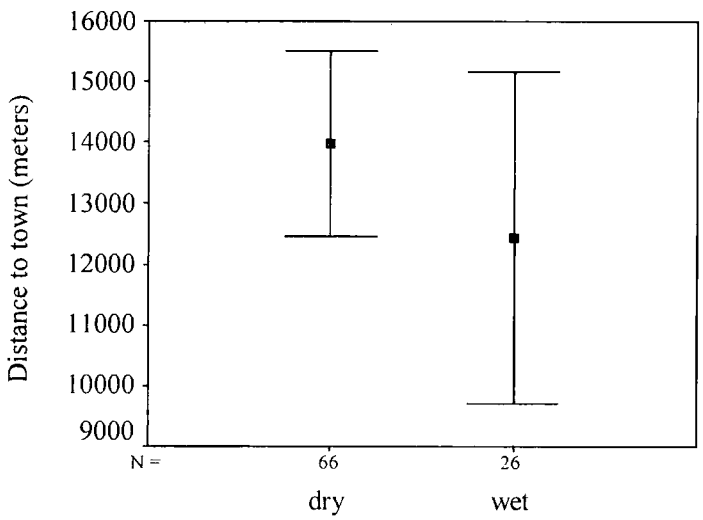

Figure 4.9. Mean and one confidence interval of distance to town for all records of deer during the dry and wet seasons in the GCR, Campeche, Mexico (both hunted and sighting data are presented).

Hunters harvested deer within a mean of 13.5 km from the village. Overall, hunters travelled an average of 2.5 kilometres longer to hunt deer during the dry season

(Figure 4.9). However, this difference is strongly influenced by the fact that they travelled an average of four kilometres longer to hunt *Mazama americana* than to hunt the other two species of deer (Figure 4.10, Table 4.1). This difference was even larger (9 km longer) during the wet season for this species (Figure 4.11) an it is highly significant statistically (Kruskall-Wallis test, $x^2 = 4.75$, df = 1, $p < 0.005$).

Hunters spent an average of 3.3 km longer travelling for hunting adults than for hunting juvenile deer (Figures 4.10 and 13; Table 4.1).

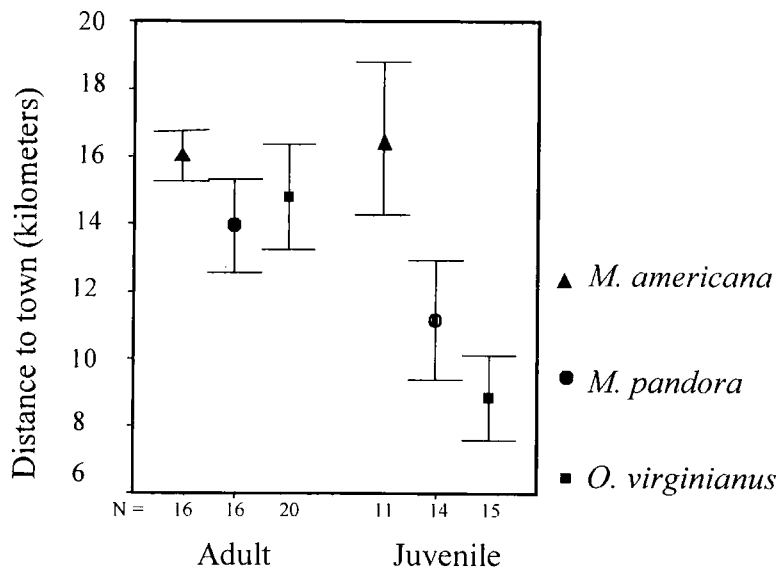

Figure 4.10. Mean and one confidence interval of distance to town for records adult and juveniles of the three species of deer in the GCR, Campeche, Mexico (both hunted and sighting data are presented).

Distances for hunting males and females were roughly equivalent and no statistical differences were found between seasons (Kruskall-Wallis test, $x^2 = 0.142$, df = 1, $p>0.5$) and species of deer (Kruskall-Wallis test, $x^2 = 0.269$, df = 1, $p>0.5$) (Figure 4.13 and 4.14). However, although differences in sexes are not statistically different, it is clear that a larger variability exist during the wet season than during the dry season in hunting distances to town of both deer hunting and sightings records (Figure 4.12).

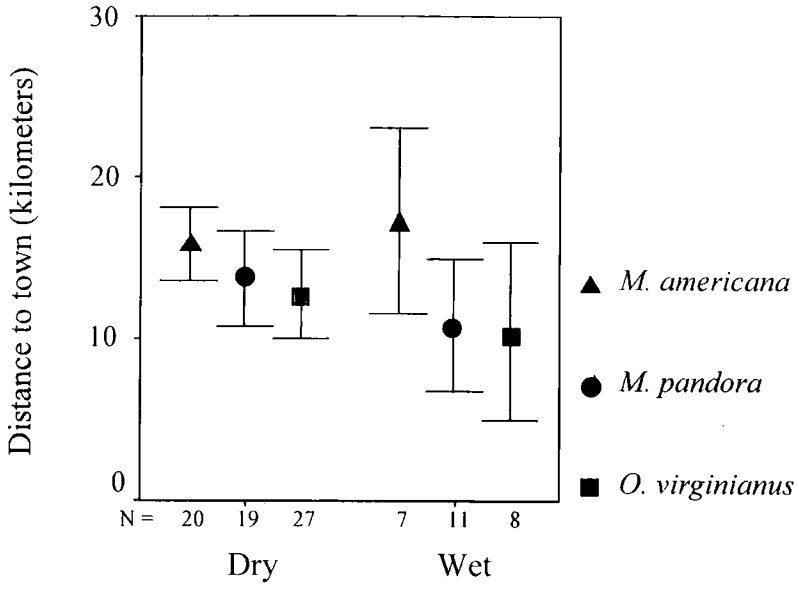

Figure 4.11. Mean and one confidence interval of distance to town for all records of the three species of deer during the dry and wet seasons in the GCR, Campeche, Mexico (both hunted and sighting data are presented).

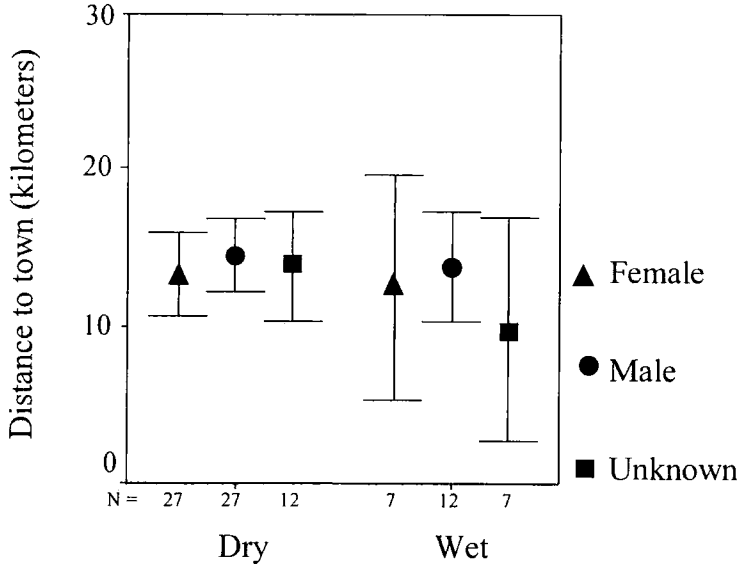

Figure 4.12. Mean and one confidence interval of distance to town for records of males and females of the three species of deer during the dry and wet seasons in the GCR, Campeche, Mexico (both hunted and sighting data are presented).

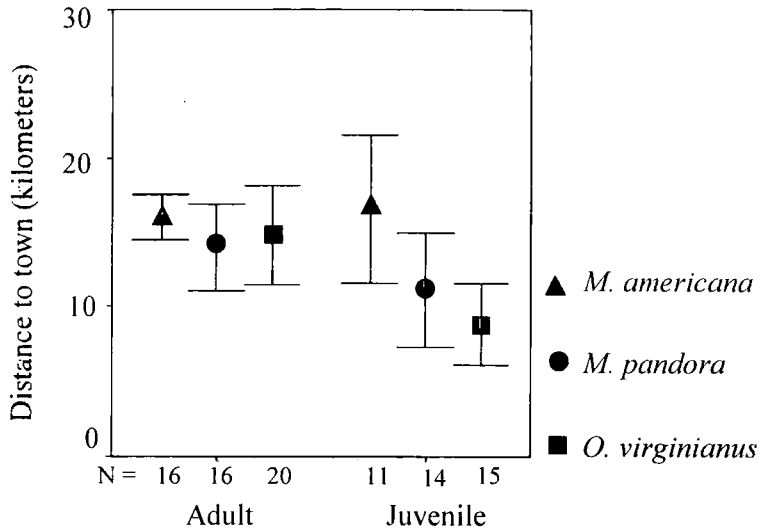

Figure 4.13. Mean and one confidence interval of distance to town for records juvenile and adults of the three species of in the GCR, Campeche, Mexico (both hunted and sighting data are presented).

4.3.3. Hunting distance to roads

Hunters harvested deer within a mean of 1.5 km from the nearest road. There were no differences in the mean distance to roads for both sets of records (hunting and sighting) between the dry and wet seasons (Kruskall-Wallis test, $x^2 = 0.130$, df = 1, $p>0.5$) (Table 4.1, Figure 4.14).

Table 4.1. Descriptive statistics (mean + one standard error in meters) of hunting distances to town and hunting distances to roads as estimated by GPS locations of deer killing and sighting points in relation with the centre of the main village (Nuevo Becal), in Calakmul, Campeche, Mexico.

Both hunting and sighting GPS records		**Hunting distance to town**		**Hunting distance to roads**	
	Sample size	Mean	Standard error	Mean	Standard error
M. americana	27	16234.5	986.9	1594.2	225.8
M. pandora	30	12642.8	1116.3	1619.4	217.5
O. virginianus	35	12246.9	1157.5	1247.9	208.9
All males	39	14378.9	913.2	1538.2	206.3
All females	34	13228.2	1184.5	1467.3	225.9
All adults	52	14916.1	768.4	1352.3	168.4
All juveniles	40	11765.4	1089.2	1624.5	187.4
All deer	92	13546.3	659.4	1470.7	125.4

The distance from the hunting site to the nearest road was roughly equivalent for the three deer species during the dry season, but it was considerably shorter for *Mazama americana* than for *Mazama pandora* or *Odocoileus virginianus* during the wet season (Figures 4.15 and 4.16). These distances were also approximately the same between seasons, species, sexes and ages with the only exception that hunters used considerably shorter distances to the roads to kill adult white-tailed deer than any other category (Table 4.1, Figure 4.15).

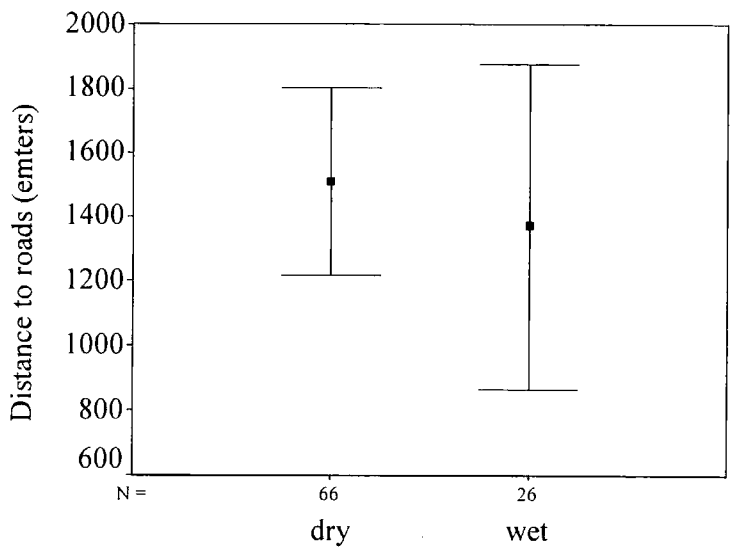

Figure 4.14. Mean and one confidence interval of distance to roads for all GPS records during the dry and wet seasons in the GCR, Campeche, Mexico (both hunted and sighting data are presented).

When straight distances to roads where compared to the estimated real hunting trails obtained with the GIS (and considering the topography of the terrain) no differences were found in total length distances obtained (Wilcoxon rank test $z = 0.34$, $df = 1$, $n = 184$, $p > 0.05$) (Figure 4.17). Overall, distances to roads presented considerably less variation than distances to town for all classes of records, both hunting and sighting observations and age and sex structure of the deer population. No major variations were found between the dry and wet seasons, with the exception already mentioned for adult white-tailed deer. Moreover, the differences in meters (range 1247 to 1624 meters) is probably biologically meaningless considering the average error of the non-differentially corrected GPS positions (200 meters in diameter). Most standard errors fell within this margin of error (Table 4.1, Figure 4.17)

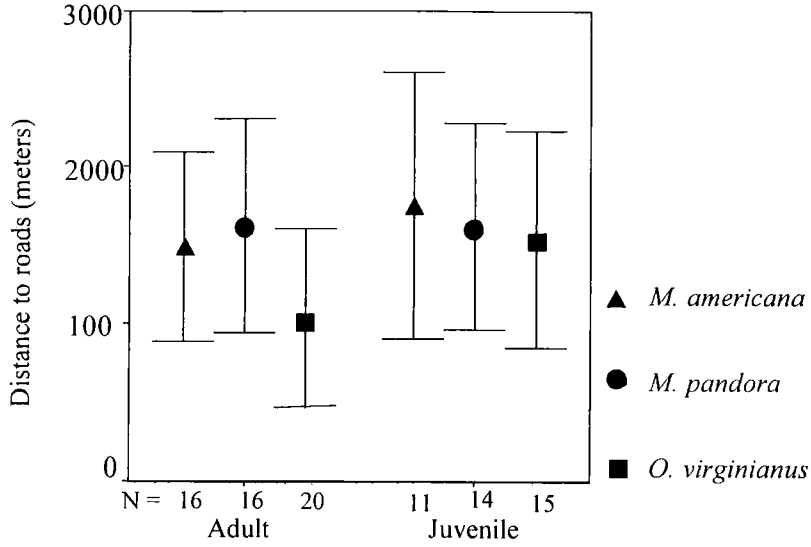

Figure 4.15. Mean and one confidence interval of distance to roads for all records of juvenile and adult deer during the dry and wet seasons in the GCR, Campeche, Mexico (both hunted and sighting data are presented).

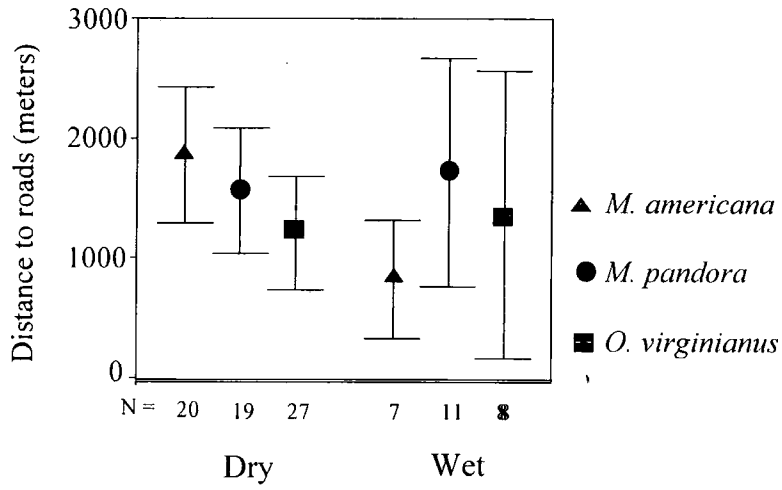

Figure 4.16. Mean and one confidence interval of distance to roads for all records of the three species of deer during the dry and wet seasons in the GCR, Campeche, Mexico (both hunted and sighting data are presented).

4.3.4. Predicting the reach of deer hunting from distances to villages

The predicted extent of hunting from the villages covered around 92% of the study area using the mean distance to town as buffer and far beyond extending even to the limits of the protected area (Calakmul Biosphere Reserve) using the upper limit confidence interval. No area is left covered by the buffers created with the lower CI of the mean in the whole of the study area. Approximately 8% of the study area is

beyond the reach of deer hunters when the mean is considered and an area equivalent to 1.5 times in size to that of the study area (203,000 ha) is potentially within the reach of hunters when the upper CI buffer is considered (Figure 4.18).

Extrapolating these same buffers to the Greater Calakmul Region provides a way to estimate the possible extent of deer hunting in the whole ecosystem. Given that the distribution of towns and villages is closely associated with major roads and with the motorway that transects the region, the buffers are also distributed in the same fashion. By creating circular buffers around the mean (13,546 km, Table 4.1) and confidence intervals obtained from the standard error (Table 4.1) of the "distance of hunting to town", it is possible to extrapolate the possible spread of deer hunting from villages, assuming that hunters in other villages behave in a similar fashion to those of the Nuevo Becal study area and that the hunter population is also equivalent. (Figure 4.19)

More than half of the whole GCR is potentially within the reach of deer hunters when the mean hunting distance to town is considered. The potential reach of deer hunting trespass the limits of the GCR and left just one third of the region potentially beyond the reach of deer hunting when the upper CI is considered. Note the incursion of buffers within the limits of the Calakmul Biosphere Reserve (protected area) polygon and how few areas are left beyond the possible influence of hunting. These areas are basically the most remote, inaccessible regions in the Calakmul Biosphere Reserve nort and south core areas (Figure 4.19).

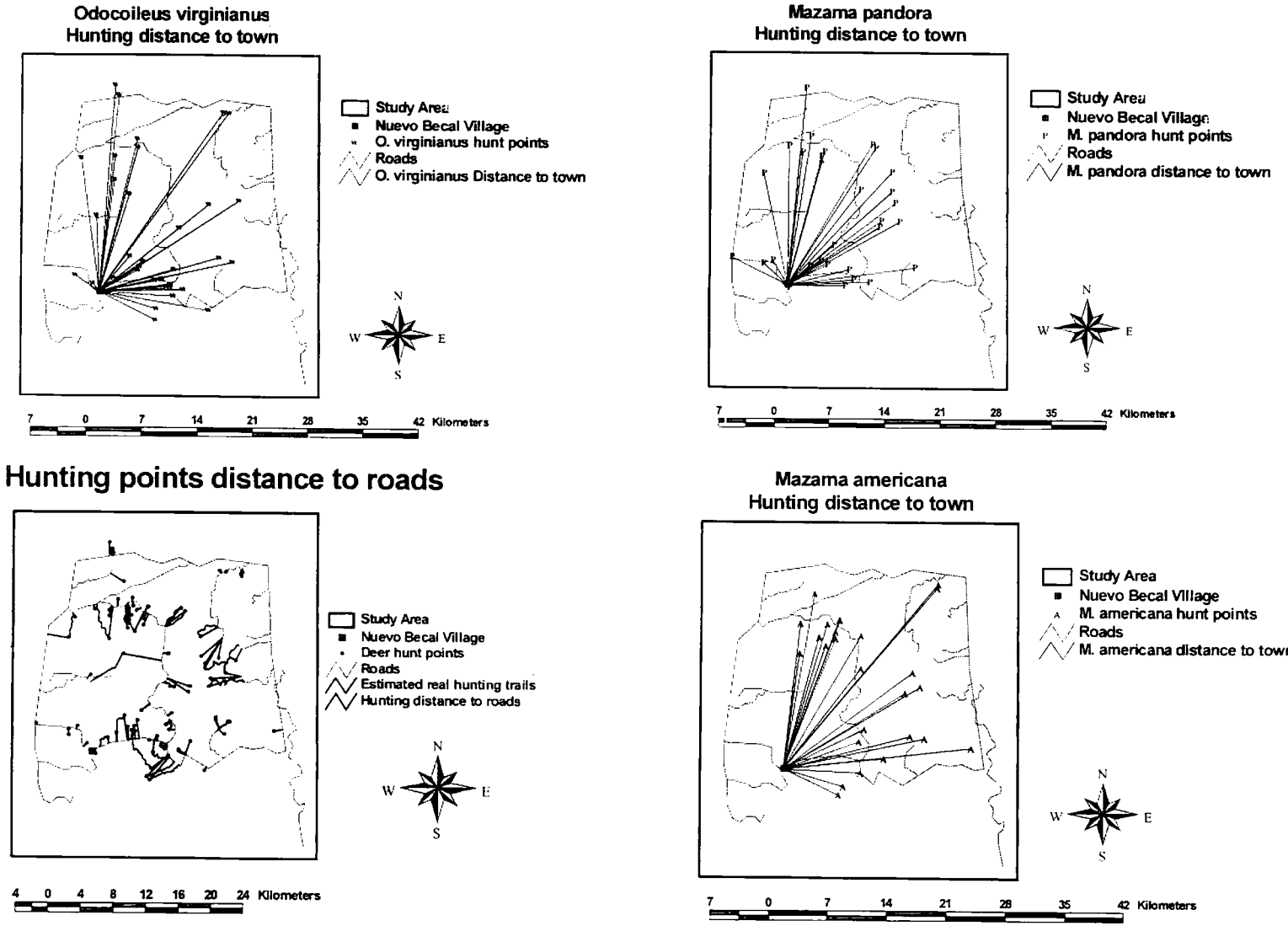

Figure 4.17. GIS-estimated deer hunting distance to town for *Mazama americana*, *Mazama pandora* and *Odocoileus virginianus* and distances to roads for all records of deer hunting in the study area, Greater Calakmul region, Campeche, Mexico

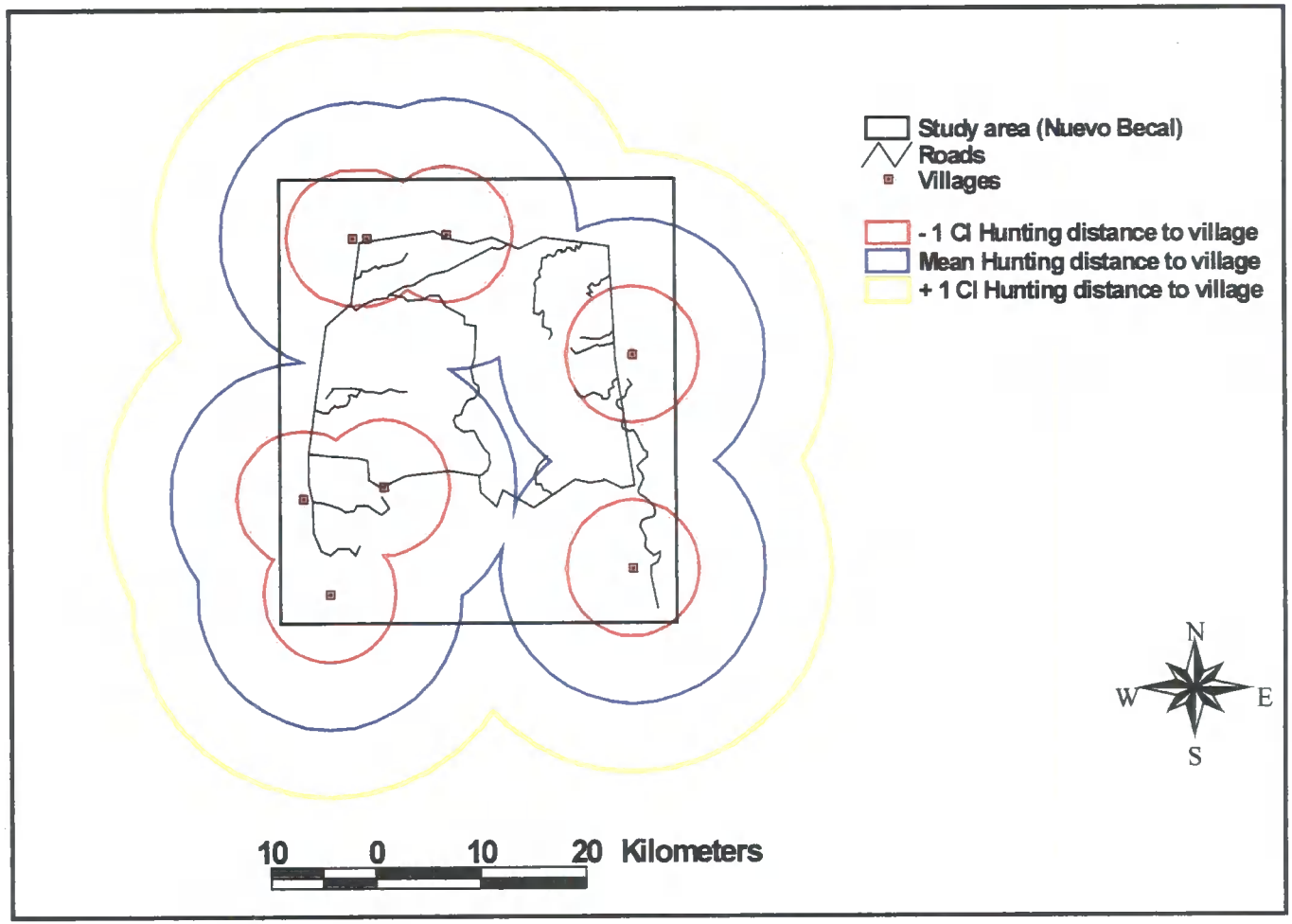

Figure 4.18. Potential extent of the reach of deer hunting in the study area and surroundings estimated by buffering the mean, upper and lower confidence interval of distance to villages, GCR, Campeche, Mexico.

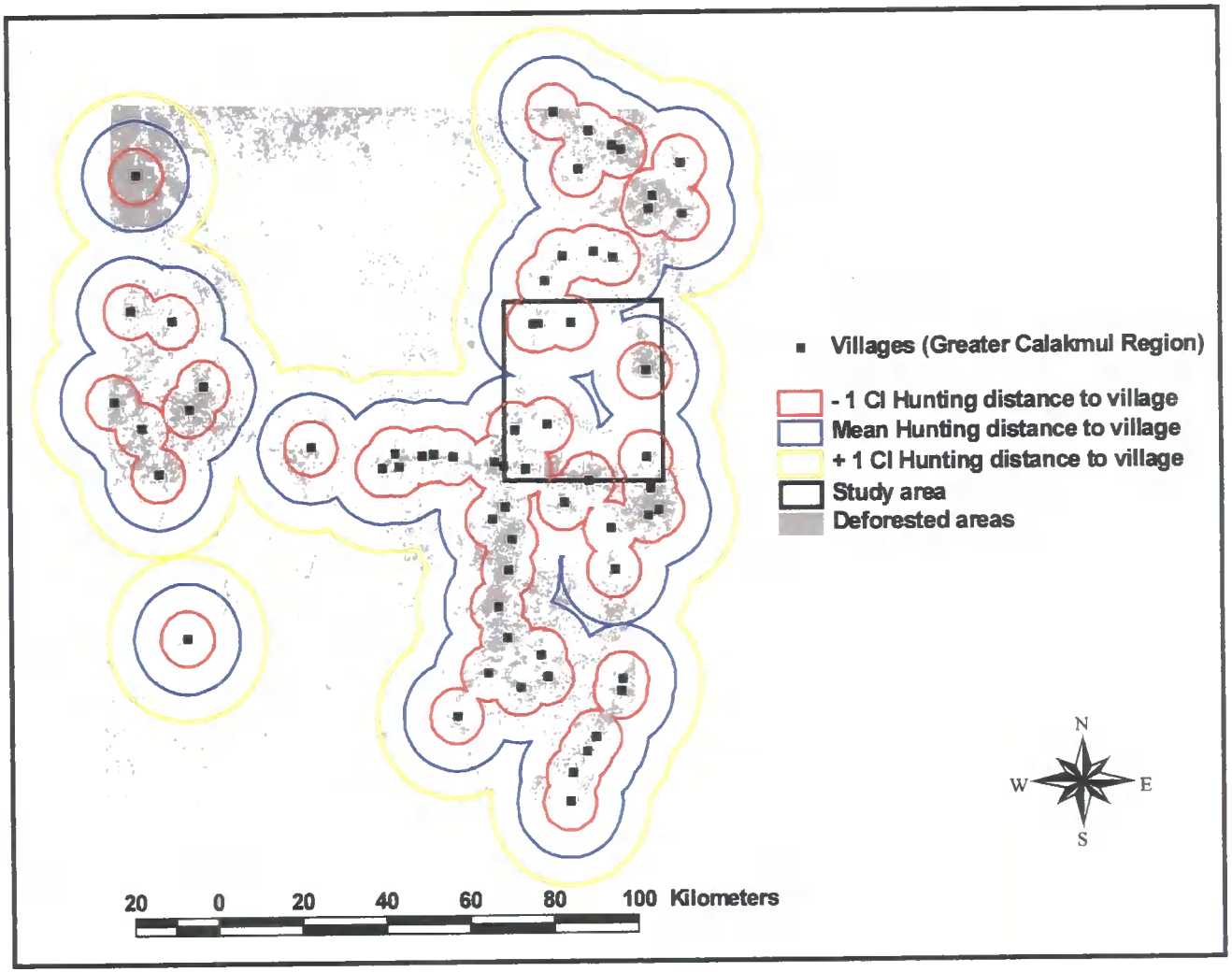

Figure 4.19. Potential extent of the reach of deer hunting in the GCR and surroundings, estimated by buffering the mean, upper and lower confidence interval of the distance to villages in the Greater Calakmul Region, Campeche, Mexico.

4.3.5. Catchments areas calculated with MCP

The size of hunting catchment areas calculated with the MCP between different species of deer was roughly equivalent (Table 4.2, Figure 4.20). However, hunters had significantly larger catchment areas during the wet season than during the dry season (Log likely-hood test G = 23.42, 2 df, $p < 0.005$) (Figure 4.20, Table 4.2).

Table 4.2. Estimation of deer hunting catchment areas with the MCP method in the study area, GCR, Mexico. Harvests rates are reported annualised for 1996-1999.

MCP Catchments	Period	Number of deer killed	Harvest deer/km^2/year	Area (ha)	Area km^2	Proportion of study area hunted (km^2)
All deer	**All**	**60**	**0.31**	**48031.8**	**48.0**	**0.30**
	Dry	26	0.18	34393.4	34.3	0.22
	Wet	34	0.21	38869.7	38.8	0.56
	1996	15	0.49	30137.4	30.1	0.19
	1997	14	0.46	30324.7	30.3	0.19
	1998	12	0.30	38987.1	38.9	0.25
	1999	14	0.33	42457.3	42.4	0.27
	2001	5	NA	NA	NA	NA
M .americana	All	18	0.18	25509.8	25.5	0.16
	Dry	10	0.14	18159.9	18.1	0.11
	Wet	8	0.14	13964.4	13.9	0.08
M. pandora	All	17	0.13	32116.1	32.1	0.20
	Dry	**11**	0.28	**10047.3**	**10.0**	**0.06**
	Wet	6	0.05	30976.5	30.9	0.19
O. virginianus	All	25	0.17	36524.4	36.5	0.23
	Dry	15	0.17	22741.6	22.7	0.14
	Wet	10	0.08	32102.5	32.1	0.20
All juveniles	All	31	0.22	35775.9	35.7	0.23
	Dry	**15**	0.23	**16324.3**	**16.3**	**0.10**
	Wet	16	0.13	31761.8	31.7	0.20
All adults	All	29	0.16	45878.5	45.8	0.29
	Dry	12	0.09	33945.7	33.9	0.21
	Wet	17	0.10	41567.3	41.5	0.26
All males	**All**	**31**	0.16	**48551.6**	**48.5**	**0.31**
	Dry	13	0.10	32342.4	32.3	0.20
	Wet	18	0.09	48123.5	48.1	0.31
All females	All	29	0.16	46132.6	46.1	0.29
	Dry	13	0.11	30975.9	30.9	0.19
	Wet	16	0.11	35127.4	35.1	0.22

The largest catchment areas were found for all deer hunting records pooled together and the largest catchement area by species of deer corresponded to the white-tailed deer followed *Mazama pandora* and *Mazama americana*. Hunters exhibited largest catchments to hunt males and adult deer than females or juvenile deer. The largest

harvest rates per hunting catchment corresponded to all deer records pooled together (0.31 deer/km^2/year), followed by *Mazama pandora* catchment area during the dry season (0.27 deer/km^2/year) and then the catchments of juvenile deer during the dry season (0.23 deer/km^2/year) (Table 4.2).

While some hunters exhibited regular catchment area sizes, others presented a large variation in their catchments (Figure 4.18). The size of the deer hunting catchment areas was statistically different between hunters and seasons (paired t test, t = 4.650, 5 df, p < 0,05) and hunters exhibited considerably larger areas during the wet season (Figure 4.20).

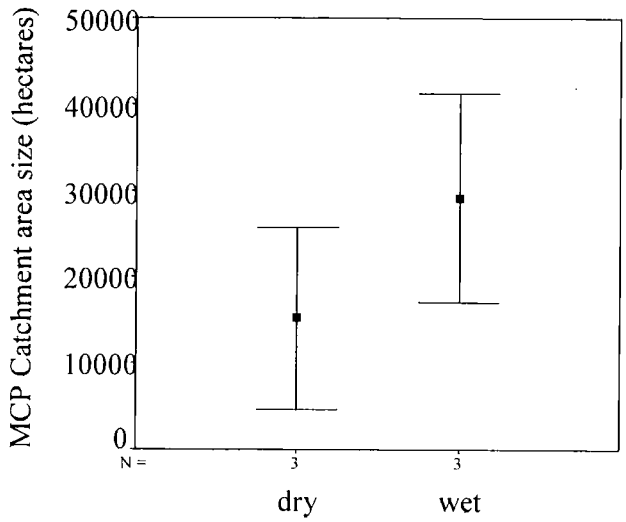

Figure 4.20. Mean and one confidence interval of the size of deer hunting catchment areas (from three hunters) estimated with the MCP method during the dry and wet seasons in the study area, GCR, Mexico.

Overall, the nine cooperating hunters in the study area exhibited a total deer hunting catchment of 48,031.8 hectares (approximately 48 km^2) where they harvested an average of 0.13 deer/km^2 from 1996 to 1999 or the equivalent of 0.03 deer/km^2/year. However, the catchment areas were significatively smaller for juvenile deer at the beginning of the study (1996 = 7571.8 ha, 1997 = 4544 ha) and increased in size at the end of the study (1998= 24611.2 ha, 1999 = 4080.2 ha and 2001 = 9081.8 ha) (two tailed t test, t = 13.22, df = 4, p < 0.005).

The distance to town from the weighted mean centroid of the annual catchment areas was marginally larger at the end of the study period than at the beginning for all deer records (two tailed t test, t = 13.22, d. f . = 4, p < 0.005) and for juvenile deer (two tailed

t test, $t = 18.34$, $df = 4$, $p < 0.005$) (Figure 4.21). Interestingly, these differences does not exist when the same analysis is performed for adult deer (Figures 4.21).

This analysis, together with the fact that juvenile deer were more frequently hunted in areas closer to the village (and therefore to agriculture and second growth vegetation areas) strongly suggest the presence of a population sink for juvenile deer around the main human settlement area.

The spatial distribution of catchment areas was also variable but most catchments were located at the centre of the study area and most appeared to have at least one vertice located around or at least close to the main human settlement (Nuevo Becal) (Figures 4.21 and 4.22). The main exception are the annual hunting catchments for juveniles and adult deer that not only were extremely variable in size but also in their spatial arrangement for the hunting of juvenile deer. While most hunting catchments of adult deer remain more or less constant in size and spatial arrangement (Figures 4.21 to 4.22), the opposite is true for the juvenile catchment areas (Figure 4.21). During the first two years of the study (1996-1997) the catchments for juveniles were comparatively small and concentrated around the main village. The next three years (1998 and 1999 and 2001) hunters exhibited considerably larger catchment areas that were located close to the village (1999), to the east and west of the village (1999) and almost 15 kilometres north of the village during 2001 (Figure 4.22). For most of the deer hunts, hunters respected the boundary of its land-hold (Figure 4.23).

This, again, is suggestive of a more complex predator-prey relationship between hunters and juvenile deer than between hunters and adult deer or any other category including the three species of deer or the sex structure of the deer populations. The combined facts that juveniles were generally hunted in areas closer to the villages than adults or any other category and that their catchments were relatively smaller and had the main village as approximate centre at the beginning of the study, but increased in size and changed location by the end of the study, is again suggestive of either a potential population sink, the occurrence of highly dynamic dispersion patterns of juvenile deer in the GCR, hunters looking for juvenile deer in a more dynamic fashion than they do for adults or simply occurring by chance.

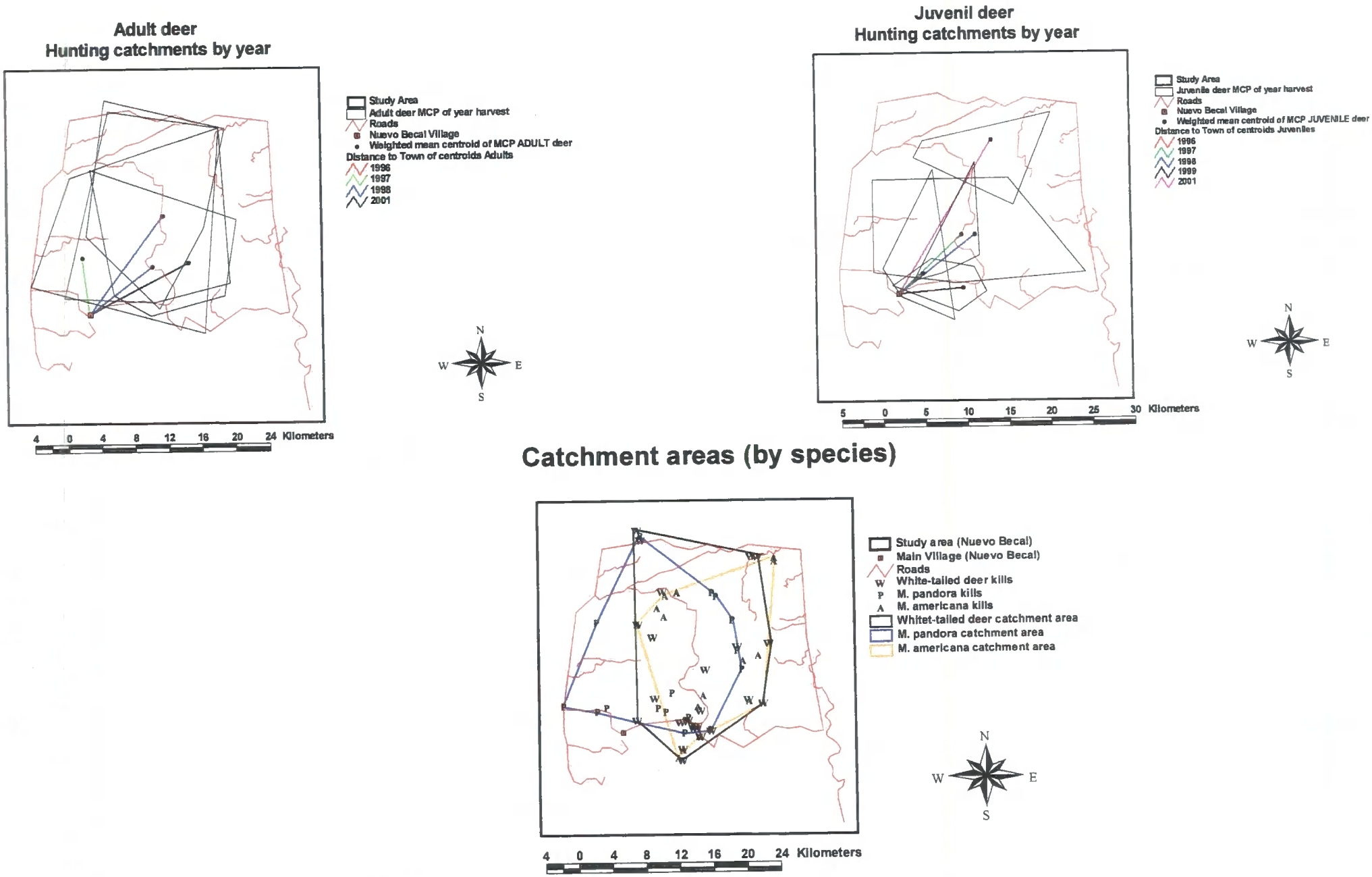

Figure 4.21. Hunter catchment areas as estimated with the MCP method by species, adult and juvenile deer in the GCR, Mexico.

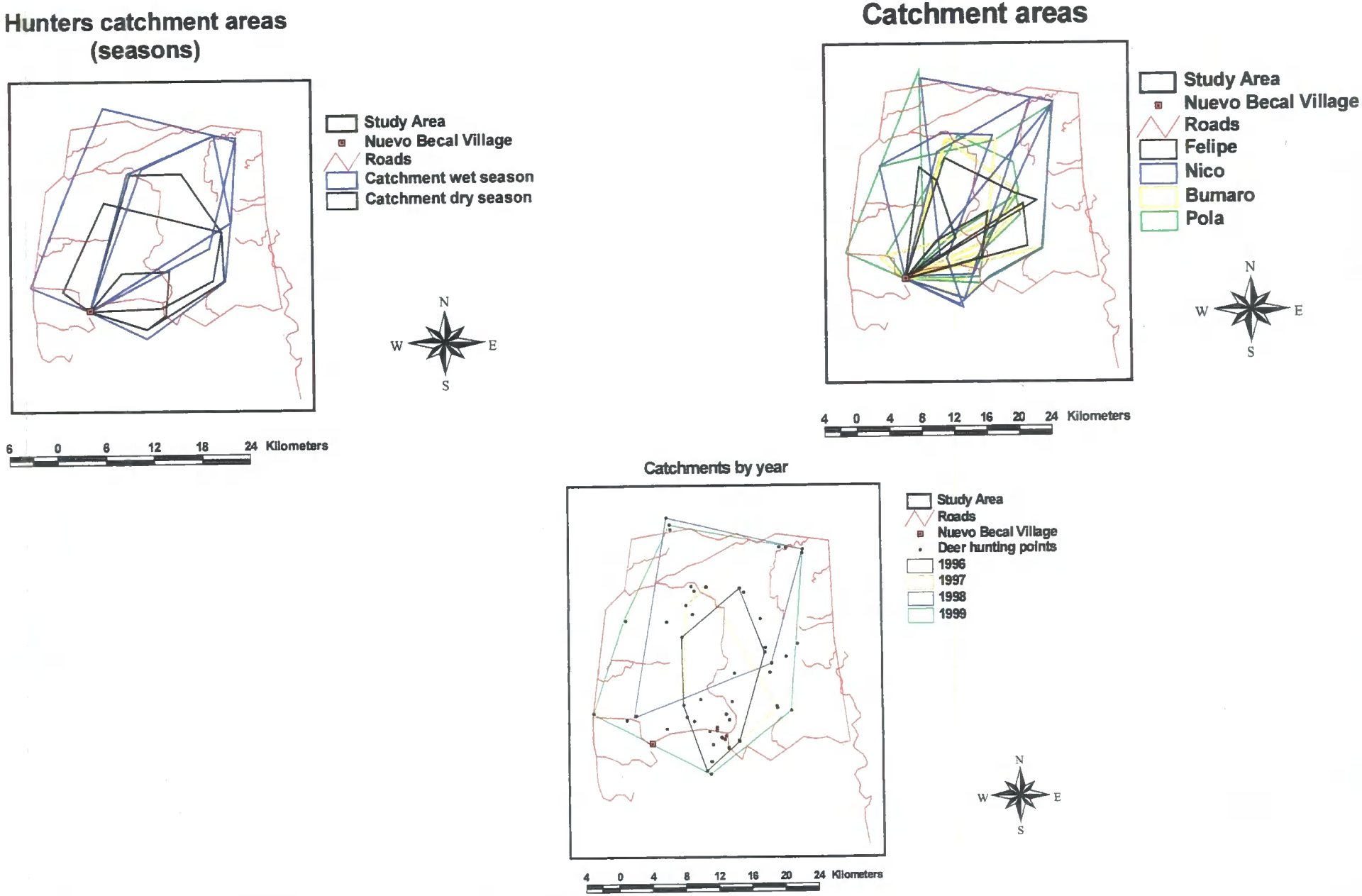

Figure 4.22. Hunting catchment areas as estimated with the MCP method by year, seasons and for four of the participating hunters in the study area, GCR, Mexico.

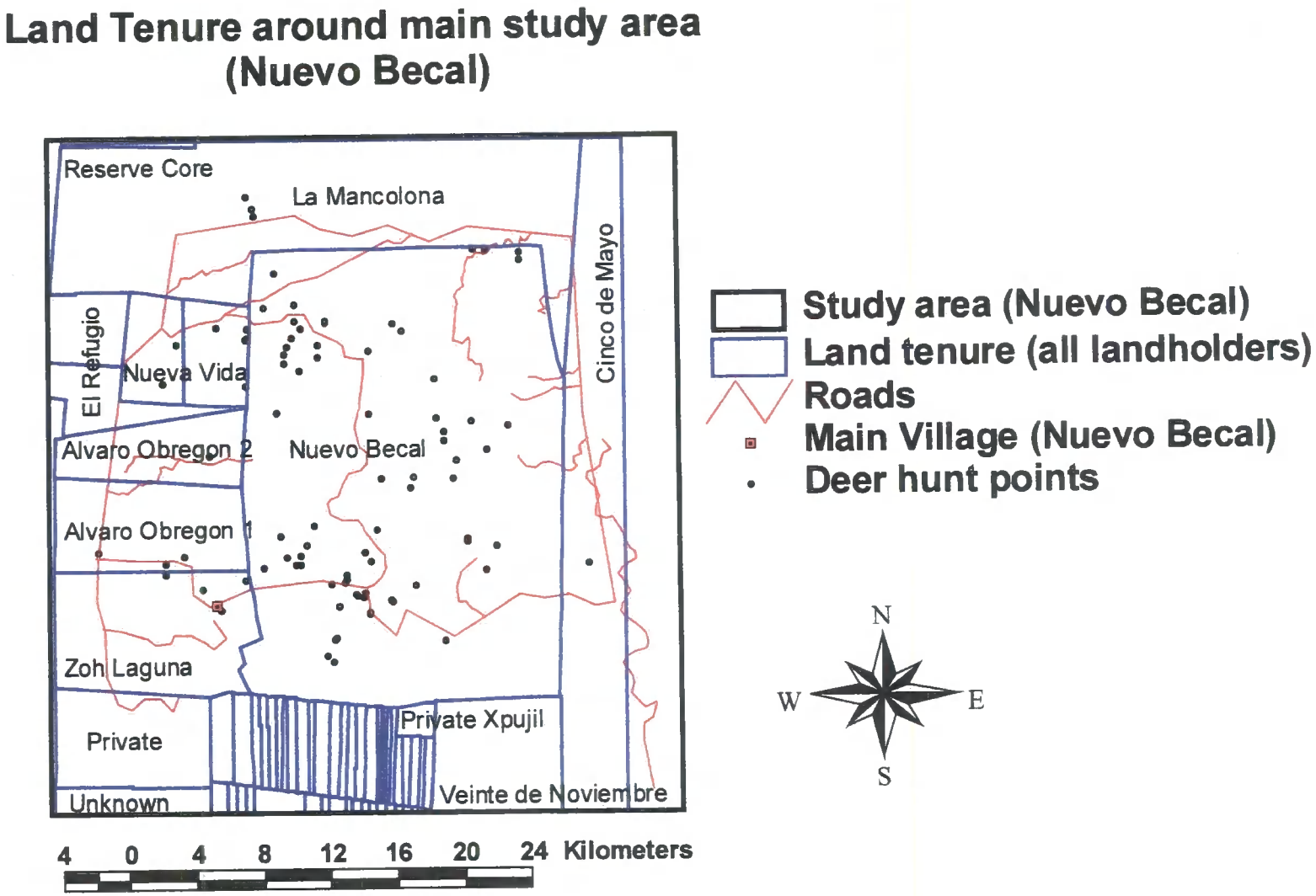

Figure 4.23. Spatial location of the deer hunting GPS positions collected from 1996 to 2001 in relation with the land tenure of the different land-holdings in the GCR, Campeche, Mexico. Most of the deer hunts took place inside of the Nuevo Becal ejido.

4.3.6. Catchments areas calculated with Adaptive Kernel (AK) method

The calculation of catchment areas rated by hunting pressure with the AK method demonstrated that hunting pressure (as rated by harvest of deer per square kilometre) is extremely variable in time and space. There was also a large variability in the size of the areas hunted and its spatial arrangement in proportion to the size of the study area (Table 4.3, Figures 4.24 and 4.25).

Table 4.3. Summary surface area cover values for the estimation of deer hunting pressure with the Variable kernel isolines method for *Mazama pandora*, *Mazama americana* and *Odocoileus virginanus* in the study area GCR, Campeche, Mexico.

	Probability (%)	C. I.	Total deer killed	Harvest deer/km^2/year	Hunting Pressure	Land Surface Area Hectares	Land Surface Area km^2	Proportion of the study area hunted km^2
Mazama pandora	85	3	3	0.005	Low	103663.7	103.6	.66
	90	2	5	0.045	Moderate	27548.3	27.5	.17
	95	1	9	0.052	High	10698.6	10.6	.06
Mazama americana	85	3	1	0.002	Low	50266.2	50.2	.32
	90	2	12	0.082	Moderate	36723.5	36.7	.23
	95	1	4	0.061	High	16101.7	16.1	.10
Odocoileus virginianus	85	3	11	0.027	Low	98352.7	98.3	.63
	90	2	4	0.095	Moderate	10170.1	10.1	.06
	95	1	10	0.571	High	4203.2	4.2	.02

The kernels were particularly variable in size, shape and spatial location within the calculation of annual hunting pressures (Figures 4.27 to 4.28) and less variable within the calculation of hunting rates of the three species of deer, juveniles, adults, males and female deer (Figure 4.28). The highest hunting pressure found was for the white-tailed deer, followed by that of *Mazama pandora* and then *Mazama americana* for the Kernel polygons of 90% probability (1 CI). This order changes for the next Kernel of 90% probability (2 CI) with the highest harvest exhibited again by the white-tailed deer but followed now by *Mazama americana* and the *M .pandora*. Finally, the lowest hunting pressure (last Kernel of 85% probability or 3 CI) was found for *Mazama americana* followed by *Mazama pandora* and *Odocoileus virginianus*. The AK that covered the largest surface area hunted in proportion with the study area was that of *Mazama pandora* with 66% of the area covered by the three polygons (Table 4.3, Figures 4.27 and 4.28). Hunters therefore, exerted a highest hunting pressure on white-tailed deer but

in a more constrained area than that of *Mazama pandora* and exhibited the lowest hunting pressure on *Mazama americana* in an even smaller surface area. (Table 4.3, Figure 4.27).

Table 4.4. Summary surface area cover values for the estimation of deer hunting pressure with the variable Kernel isolines method for all species of deer pooled in male, female, adult and juvenile categories. The "All deer" category represent the Kernel polygon for all deer groups pooled together and the "All deer (LS validated)" is the final least square validation for the Kernel estimation.

	Probability (%)	C. I.	Total deer killed	Harvest deer/km²/year	Hunting Pressure	Surface area ——— Hectares	Surface area ——— km²	Proportion of the study area hunted km²
Males	85	3	7	0.030	Low	55240.7	55.2	.35
	90	2	15	0.203	Moderate	18561.4	18.5	.11
	95	1	8	0.483	High	4127.60	4.11	.02
Females	85	3	5	0.018	Low	66545.1	66.5	.42
	90	2	11	0.133	Moderate	20473.9	20.4	.13
	95	1	13	0.600	High	5400.70	5.41	.03
Juveniles	85	3	5	0.023	Low	54548.7	54.5	.35
	90	2	17	0.210	Moderate	20259.6	20.2	.13
	95	1	15	0.700	High	5782.01	5.70	.03
Adults	85	3	12	0.053	Low	55973.3	55.9	.36
	90	2	21	0.300	Moderate	16936.6	16.9	.10
	95	1	21	0.920	High	5778.10	5.71	.03
All deer non validated	85	3	16	0.068	Low	58526.3	58.5	.37
	90	2	18	0.233	Moderate	19256.8	19.2	.12
	95	1	25	1.008	High	6211.30	6.21	.04
All deer LS validated	85	3	**19**	**0.190**	**Low**	**247609.1**	**24.7**	**.16**
	90	2	**21**	**0.400**	**Moderate**	**132038.8**	**13.2**	**.08**
	95	1	**20**	**1.425**	**High**	**35656.8**	**3.5**	**.03**

The females presented a larger surface area of the AK polygons than the males, but juvenile and adult AK area polygons were roughly equivalent in size. This suggest that hunters extended their ranges larger when hunting females than males, but had equivalent hunting ranges for hunting adult and juvenile deer (Table 4.4, Figure 4.29).

The spatial allocation, shape and size of hunting pressure areas varied within this categories with some areas presenting just one polygon of high and moderate hunting pressures, while others presented two or more spatially independent polygons or one major large polygon and several small satellite polygons (Figures 4.26 to 4.29).

However, the majority of calculated high hunting pressure polygons were located in the surroundings of the main human settlement (Nuevo Becal) with the notable exception of the high hunting pressure kernel of *Mazama americana*, that was located about 15 km away from the settlement in the northeast of the study area (Figure 4.28 and 4.29).

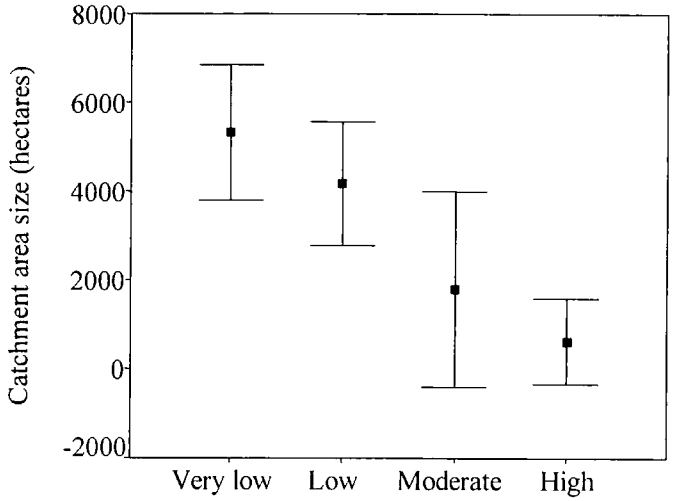

Figure 4.24. Total surface area of Kernel polygons rated as exhibiting low, moderate and high hunting pressure areas for all deer records in the study area, GCR, Mexico.

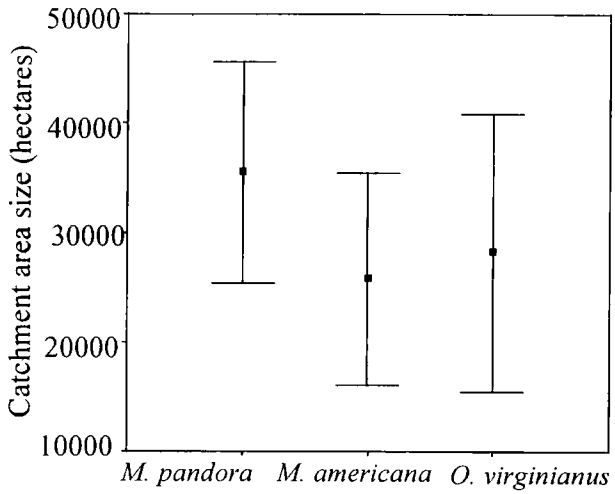

Figure 4.25. Total surface area of Kernel polygons of the three species of deer (*Mazama americana*, *Mazama pandora* and *Odocoileus virginianus*) for all deer records in the study area, GCR, Mexico.

Mazama pandora experienced the largest extent in surface area hunted for the high and moderate hunting pressures while the white-tailed deer presented the smallest and *M. americana* intermediate values. The white-tailed deer however, depicted the largest extent of the low hunting pressure area if the overlapping of the other two categories (high and moderate) is not considered (Figure 4.29, Table 4.3).

When all deer are pooled together for a sex and age analysis of hunting pressure, the largest extent of the high hunting pressure area correspond to female and juvenile deer respectively. Females received a larger extent of low hunting pressure areas than males, but males received an slightly larger moderate hunting pressure area. For both males and females the high hunting pressure areas centred around the main human settlement, with a few small satellite areas for the males (Figures 4.28, Table 4.4). Juvenile deer presented the second highest (after *Mazama pandora*) hunting pressure area. The kernels for juveniles were highly centred around the main human settlement area with no satellite isophlets for this category (Figure 4.28, Table 4.4).

The annual catchment areas calculated with the AK technique demonstrated that hunting pressure can be an extremely variable concept in time and space. Conversely to the results obtained with the calculation of catchment areas with the MCP method, the annual catchments of hunters calculated with this technique varied considerably not only in size and extent but in its spatial arrangement. The first two years of the study (1996-1997) the high hunting pressure areas were small and centred around the main human settlement while during 1998, both moderate and high hunting pressure areas were located northwest and northeast to the village. During 1999 the hunters concentrated their activities to the east of the study area but the extent of their hunting catchments was almost two-fold from that of the three previous years (Figures 4.28 and 4.29). The proportion of sexes harvested during the years was also uneven. While in 1996 and 1997 the proportion was similar (7M: 8F and 7:7 respectively), during 1998 more males were harvested (7M: 5F) and similarly for 1999 (8M:6F). Of this harvest, more juveniles were harvested during the first two years of the study (1996-1997, 22 juveniles and 11 adults) than during the last two years (1998-1999, 9 juveniles and 18 adults). Once again, this is suggestive that considerable variation exist in the temporal patterns of deer harvesting exhibited by this group of hunters.

The two final AK analysis provide a general picture of deer hunting pressure for all deer categories pooled together. According with this estimation, the overall extent of hunting pressure covered around 54% of the study area (approximately 84 of 155 km^2) with two high hunting pressure areas (one around the main human settlement) and two large moderate hunting areas. Together, the high and moderate hunting pressure areas covered around 25 km^2 (or around 30% of the study area) and the low hunting pressure area covered 58.5 km^2 (or around 69% of the study area) (Figure 4.30, Table 4.4).

The least square validation method (LSV) produced the final map for the calculation of hunting pressure in the study area. The main differences between the maps produced with and without the LSV (Figure 4.30) are that the three original moderate hunting pressure areas where pooled into just two areas and that the size and extent of both low and high hunting pressure areas was slightly reduced to approximately 4.5 % of the LSV map (Figure 4.30). According to this last AK model it can be calculated that the hunters that participated in the study from 1996 to 1999 were harvesting deer in the area at a rate of approximately 1 deer/km^2 in 16% of the study area (25 of 155 km^2), between one and two deer/km^2 in 1% of the study area (approximately 15 of 155 km^2) and more than 5 deer/km^2 in 0.03% of the study area (4.7 of 155 km^2). This represent a combined surface area covered by the hunters equivalent to 32% of the study area. Deer was not hunted at all in the remaining 68% of the study area by the hunters that cooperated with this information (Table 4.4).

It is noteworthy to point out that all AK polygons extended far beyond the limits of the Nuevo Becal community and in some cases even far beyond the limits of the study area. This is interesting, cause we have to remember that the AK were obtained with a thorough but limited amount of data provided by a relatively small proportion of the population of human hunters within the study area.

Assessment of sustainable deer hunting rates and quotas

The estimation of hypothetical sustainable harvests with the the "Production Model" (Robinson and Redford 1991) and the "Harvest Model" (Hurtado-Gonzalez and Bodmer 2004) suggested that hunting of both Mazama species (pooled together for the analysis) and the white-tailed deer is sustainable given the current average harvest rates (Table 4.5). The production model (H/P) provided estimates well above the maximum fraction of production (MFP) than can be sustainable harvested for both deer. The harvest model suggested harvest rates that are at or slightly above the MFP for *Mazama* spp. And below for the white-tailed deer.

Table 4.5. Assessment of hunting sustainability of ungulate populations in the study area (Nuevo Becal village), GCR, Campeche, Mexico trough the "Production model" (Robinson and Redford 1991) and the "Harvest model" (Hurtado-Gonzalez and Bodmer 2004).

Species	Density[a] ind/km^2	P[b] ind/km^2	P_{max}[c] ind/km^2	Harvest rate[d] ind/km^2	H/P_{max}	H/P	MFP[e]	Sust[f]
Mazama spp.	0.49	0.11	0.09	0.047	0.52	0.42	0.4	Yes
O. virginianus	0.015	0.20	0.18	0.038	0.21	0.19	0.4	Yes
Total	0.505	0.327	0.27	0.085				

a. Based on actual densities estimated in the study area from 1996-2001. An average from densities obtained in permanent and temporary transects is used. Densities of both Mazama species *(Mazama pandora* and *Mazama americana)* were pooled as sample sizes of sightings were too small for individual calculations (but see Table 2.1 in Chapter 2).
b. Productivity (young/female/km2) based reproductive data from Hurtado-Gonzalez and Bodmer (2004) and Naranjo (2002).
c. P_{max} data from Hurtado-Gonzalez and Bodmer (2004) and Naranjo (2002)
d. Average harvest rates as calculated for the whole study area plus a 10% error added to compensate for non-recorded data.
e. Hypothetical maximum proportion of the production that can be sustainably harvested (Robinson and Redford 1991)
f. Hypothetical sustainability attained or not.

The calculation of "Maximum annualised harvest rates" (MAH) for deer in the hypothetical source and sink areas obtained with the Kernel method to calculate catchment areas of hunters provided rather high harvest rates that probably would not be sustainable for long if conservative estimates as those provided by the Robinson and Redford (1991) and Hurtado-Gonzalez and Bodmer (2004) methods are used (Table 4.6). However, we have to remember the dynamic nature of hunting in this areas (Figure 4.29) that probably lesser the detrimental effect of hunting through a constant immigration and recruitment of deer. The source-sink dynamics model applies well for *Mazama pandora* and the *Odocoileus virginianus* where more animals were harvested in

"sink" areas than in source areas, but not for *Mazama americana* where more animals were harvested in "sources" than in "sinks" (Table 4.6)

Table 4.6. Maximum annualised harvest rates (MAH) of deer in "sources" and "sink" areas calculated with the Kernel probabilistic method, total number of deer killed per area (from 1996-1999 from figures 4.27 and 4.28) and whether the assumption of the source-sink dynamics were accomplished or not (when harvest in sinks > harvest in sources, number of juvenile > number of adult deer).

	Area	Total deer killed	Adult/juvenile ratios		MAH deer/km²/year	Sust[1]	S-S dynamics accomplished[2]
			Adult	Juv			
M. pandora	total	17	8	9	0.970	no	yes
	sources	5	4	1	0.045	yes	
	sinks	12	4	8	0.052	yes	
M. americana	total	17	9	8	0.130	yes	no
	sources	10	5	5	0.078	yes	
	sinks	7	4	3	0.052	yes	
O. virginianus	total	25	13	12	0.685	no	yes
	sources	7	6	1	0.092	yes	
	sinks	18	7	11	0.593	no	

1. Sustainability was considered accomplished when harvest rates do not exceed 0.6 of the potential P_{max} for neotropical deer according with the Robinson and Redford (1991) production model.
2. The theoretical dynamics of a source-sink system was considered accomplished when mortality (harvest) was lower in sources than in sinks.

4.3.7. Estimating the extent of deer hunting pressure within the villages

The results of intensive interviews and meetings with administrative authorities as well as the extensive collection of field notes from encounters with individual hunters in the five major human land-holds within the study area from 1996 to 2001, demonstrated that the nine participating hunters in the Nuevo Becal community are probably among the top deer hunters in the whole of the study area.

The overall proportion of potential deer hunters against the total number of man in working ages is relatively high in the study area (mean 23%). However, a relatively small proportion of these potential deer hunters were assessed as having similar overlapping patterns (e.g. similar hunting grounds, similar hunting intensity) to those of the nine cooperating hunters that provided the information for this research. Of these, five hunters belonging to the same community (Nuevo Becal) as the cooperating hunters and another fifteen belonging to another two different communities were identified as having potentially similar hunting patterns to those of the hunters intensively studied. The remaining deer hunters in the study area, are either casual hunters or opportunistic

garden hunters that perform most of their hunting activities while farming and tending their crops. (Table 4.5).

Table 4.7. Results of the estimation of potential community-wide deer hunting intensity in the five major human settlements within the study area, GCR, Campeche, Mexico. Estimates based on interviews with local community authorities.

	Nuevo Becal	El Refugio	Nueva Vida	La Mancolona	Alvaro Obregon
Land-holding size (km^2)	52.5	5.5	2.4	24.2	40.5
Total number of households	58	75	28	105	≈250
Total number of men of working ages	≈ 75	≈ 60	≈ 40	≈ 90	≈ 120
Estimated number of potential hunters	≈ 60	≈ 30	± 15	≈ 70	≈ 60
Estimated number of active deer hunters	15	8	5	≈ 30	≈ 20
Average family size	5	4	5	7	4
Proportion of potential deer hunters/working man	0.25	0.13	0.12	0.33	0.33
Estimated number of man with overlapping hunting patterns with those of cooperating hunters.	5	0	0	≈ 10	≈ 5

Deer hunting in the study area seems to be unrelated with the land-holding size, but it can be said that in general, the larger the land-holding size the larger the proportion of deer hunters (Table 4.7). In this way, a potential number of twenty extra deer hunters may have had exerted the same or at least similar hunting pressure in time and space over deer populations within the study area. The potential number of casual and opportunistic garden deer hunters (Naughton-Treves, 2002) is much more difficult to assess though, but the number is likely to be at least an order of magnitude larger (Table 4.7).

If this twenty extra hunters harvested deer at a rate similar to that exhibited by the nine participating hunters, then the overall deer harvest could had been at least two-fold to that documented here. Where and when do they harvested deer during this period is impossible to ascertain, but given the mostly solitary nature of specialized deer hunting in the region it is unlikely that it would had been in the same areas, with the same intensity and during the same time periods such as those of the hunters intensively studied. However, the overlapping of catchments of individual hunters was relatively high as calculated with the MCP method (Figure 4.22), therefore some overlapping

might had happened with at least those five other top deer hunters not willing to cooperate but living in the same place as the cooperating hunters from the Nuevo Becal community.

Table 4.8. Differences in deer hunting success with the three different hunting methods used by villagers in Nuevo Becal from 1996-2001.

	Total number of hunting events (n = 60 GPS records)	*M. americana* *(n = 18)*	*M. pandora* *(n = 17)*	*O. viginianus* *(n = 25)*
Stalking	54	16	16	22
Drives with dogs	5	2	1	2
"Sit-and-wait"	1	0	0	1

The effect of different deer hunting methods was minimal or non-existent at least within this sample of hunters, because most deer was hunted by stalking solo hunters. Only six deer from a total of 60 geo-referenced records were harvested with methods other than stalking. (Table 4.8). No further statistical analysis was considered necessary.

When a 10% error (as possible missing data) is included in the calculation of harvest rates, the total harvest increases considerably for the three species of deer (Table 4.9). It is unlikely that this error would had been larger than the 10% estimate because close monitoring of the hunting activities of the participating hunters guaranteed that most deer killed were actually recorded.

Table 4.9. Calculation of deer harvest rates with GPS records, all hunting deer records and all hunting deer records plus a 10% estimated error of missing data from 1996 to 2001, extrapolating for the whole study area disregarding the spatial and temporal arrangement of hunter's catchment areas.

Harvest rates for the whole study area (155 km^2)	Just GPS records (n = 60)		All deer hunting records (e. g. GPS, skulls, stomachs) (n = 75)		All deer hunting records + 10% error (n = 83)	
	Deer killed	Harvest deer/km^2/year	Deer Killed	Harvest deer/km^2/year	Deer killed	Harvest deer/km^2/year
All deer	60	0.095	75	0.120	83	0.133
M. pandora	17	0.025	26	0.040	29	0.045
M. americana	18	0.028	28	0.045	31	0.050
O. virginianus	25	0.040	21	0.033	23	0.038

4.3.8. Estimating deer abundance spatial indices

The resulting map of deer spatial abundance Kernel isolines, covered a large proportion of the sampled terrain and approximately 82% of the study area (Figure 4.30). Six of the transects were located completely in areas were deer abundance was high. Two partially fell in these areas. Ten transects fell partially in areas with moderate deer abundance and another six transects were located in areas with low or very low deer abundance (including one transect where zero deer signs were recorded).

The areas of high deer abundance covered approximately 0.9% of the study area (or 13.5 of 155 km^2). The areas of moderate deer abundance covered approximately 25 % (or 39 of 155 km^2) and the remaining low and very low deer abundance areas covered a combined surface of approximately 66% (or 100 of 155 km^2) of the study area. The resulting five areas depicted as with high deer abundance were located away from most human settlements with the exception of the La Mancolona village (north of the study area) that fells in an area depicted as having moderate abundance of deer (Figure 4.46). Remarkably, the areas around the main human settlement (Nuevo Becal village) were found as having moderate deer abundance, despite the fact that most hunting take place in these areas and that it has probably been heavily hunted for many years in the past. Also of interest was the finding of two areas found as presenting high and moderate deer relative abundances to the north and east of the main human settlement, but that received a much smaller proportion of the deer hunting pressure than the rest of the study area (Figure 4.30).

A multiple regression analysis attempted to explain spatial differences in deer abundance suggested that habitat heterogeneity (incorporating as independent variables the within-buffer composition of habitat types in all deer hunting geo-referenced positions) and the spatial variation in hunter induced mortality (incorporating as dependent variables the straight-line distance from GPS points to the village, the distance from GPS points to main dust roads and the individual hunter-induced mortality) suggested that habitat heterogeneity is not responsible for this variation (no statistical differences found for both *Mazama* deer). The only exception was the relationship kept among white-tailed deer, straight-line distance to town (Nuevo Becal village) and "deforested areas" (both

agricultural areas and second growth vegetation pooled) were a strong direct relationship exists and the abundance of *O. virginianus* can be predicted to increase as distance to the village (log_n transformed data) and "deforested" areas also increase (r = 0.449, r squared = 0.202, d. f. for vegetation = 4, d. f. for deer species = 2, Durbin-Watson correction for log transformed data, $p < 0.001$) (Figure 4.26)

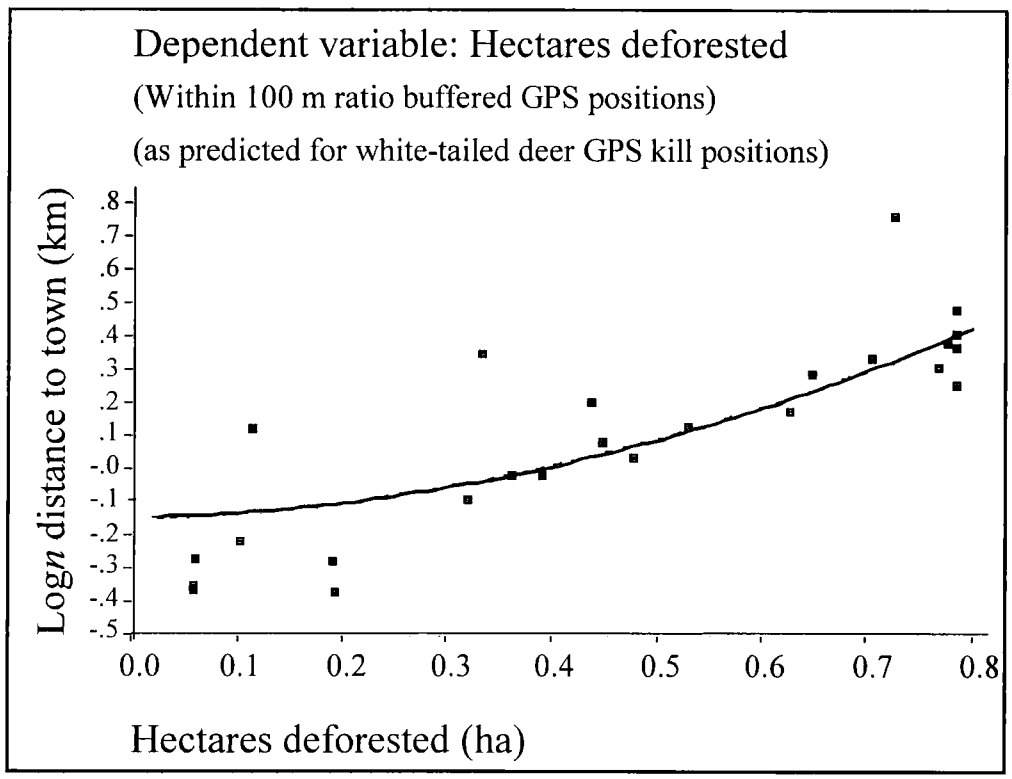

Figure 4.26. The relationship (from a Multiple Regression analysis) between white-tailed deer (*Odocoileus virginianus*) hunter-induced mortality, straight line distance to town (Nuevo Becal village) and deforested areas (both agricultural and second growth vegetation areas as part of the habitat heterogeneity composition of within-buffered 100 meters ratio of GPS killing positions) in the study area, GCR, Campeche, Mexico.

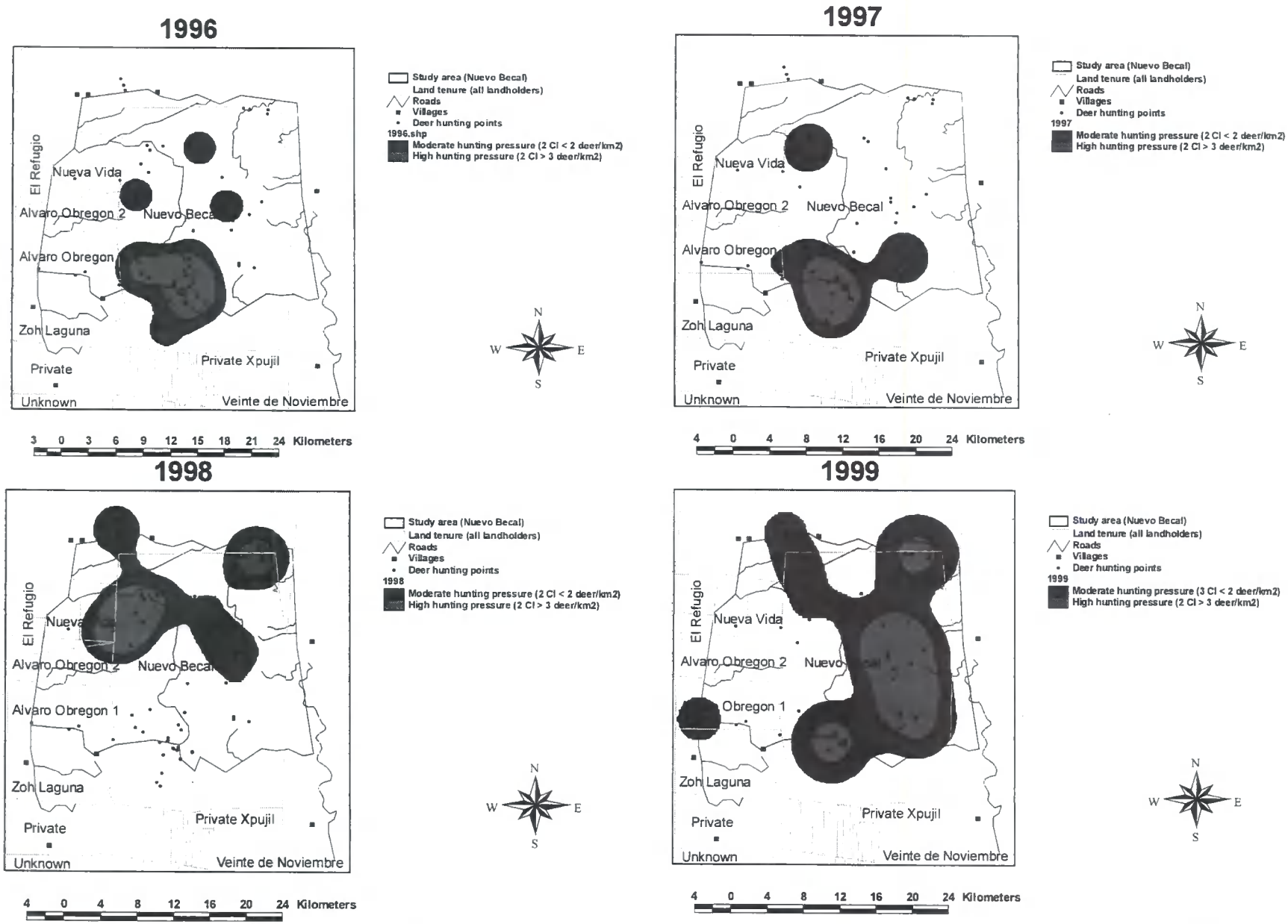

Figure 4.27. Annualized hunting pressure (high and moderate) areas during 1996 to 1999 as estimated by AK for all deer hunting records in the study area, GCR Mexico. Low hunting pressure polygon omitted to accentuate temporal variation in distribution of catchments by years.

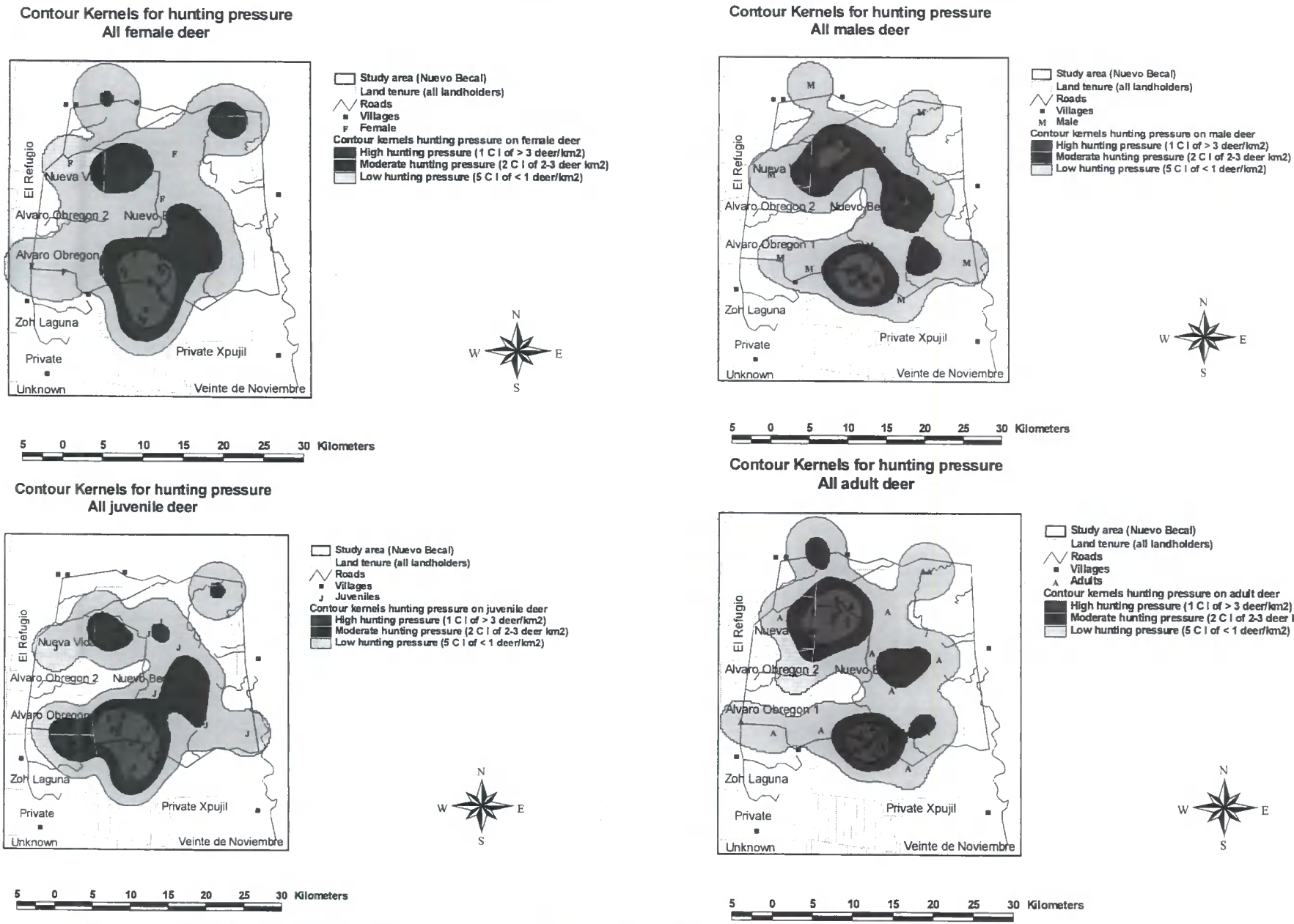

Figure 4.28. Hunting catchment areas by hunting pressure for male deer (three deer species pooled) estimated by AK for all deer hunting records in the study area, GCR Mexico.

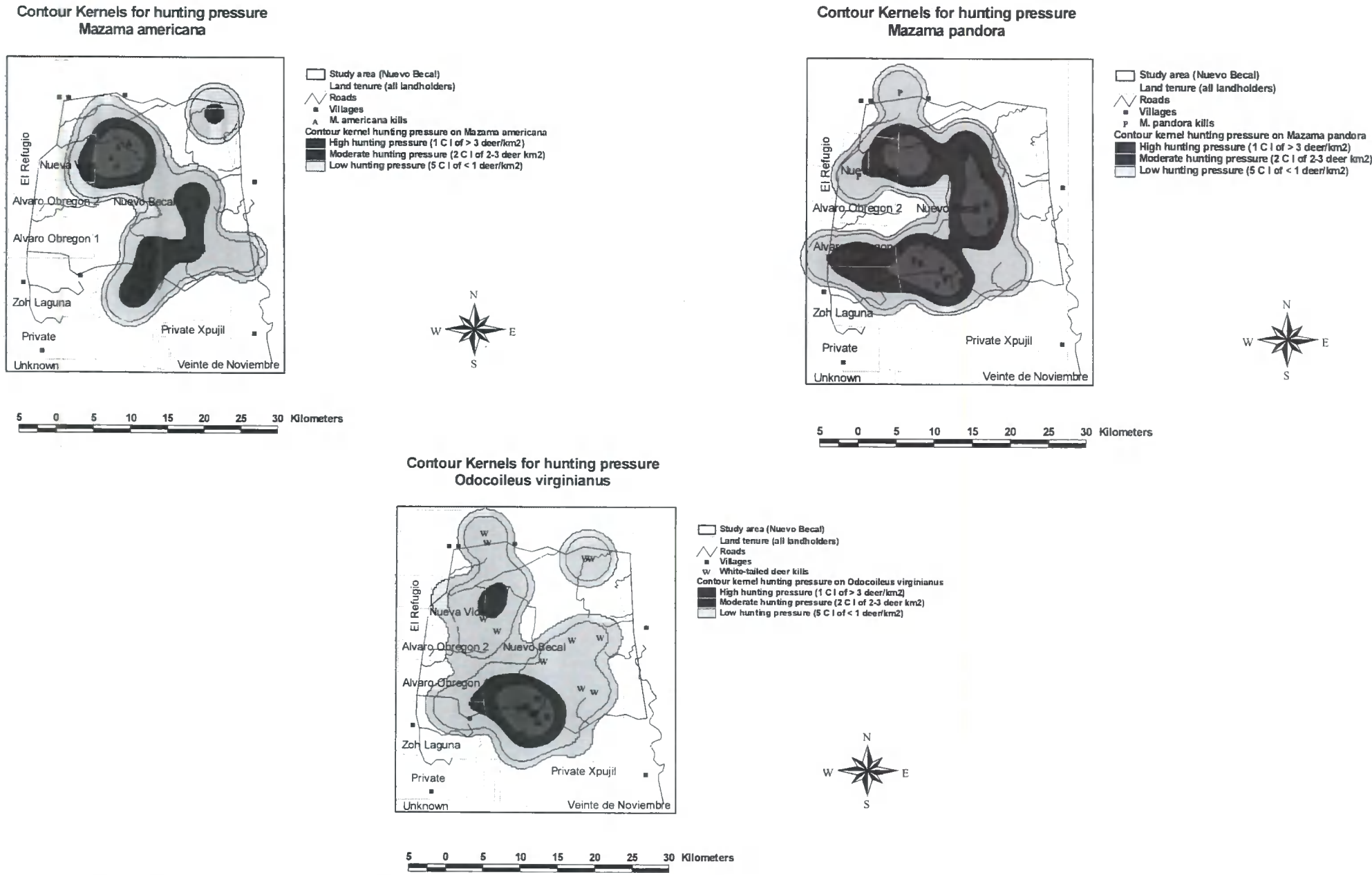

Figure 4.29. Hunting catchment areas by hunting pressure for *Mazama americana*, *M. pandora* and *O. virginianus* in the study area, GCR.

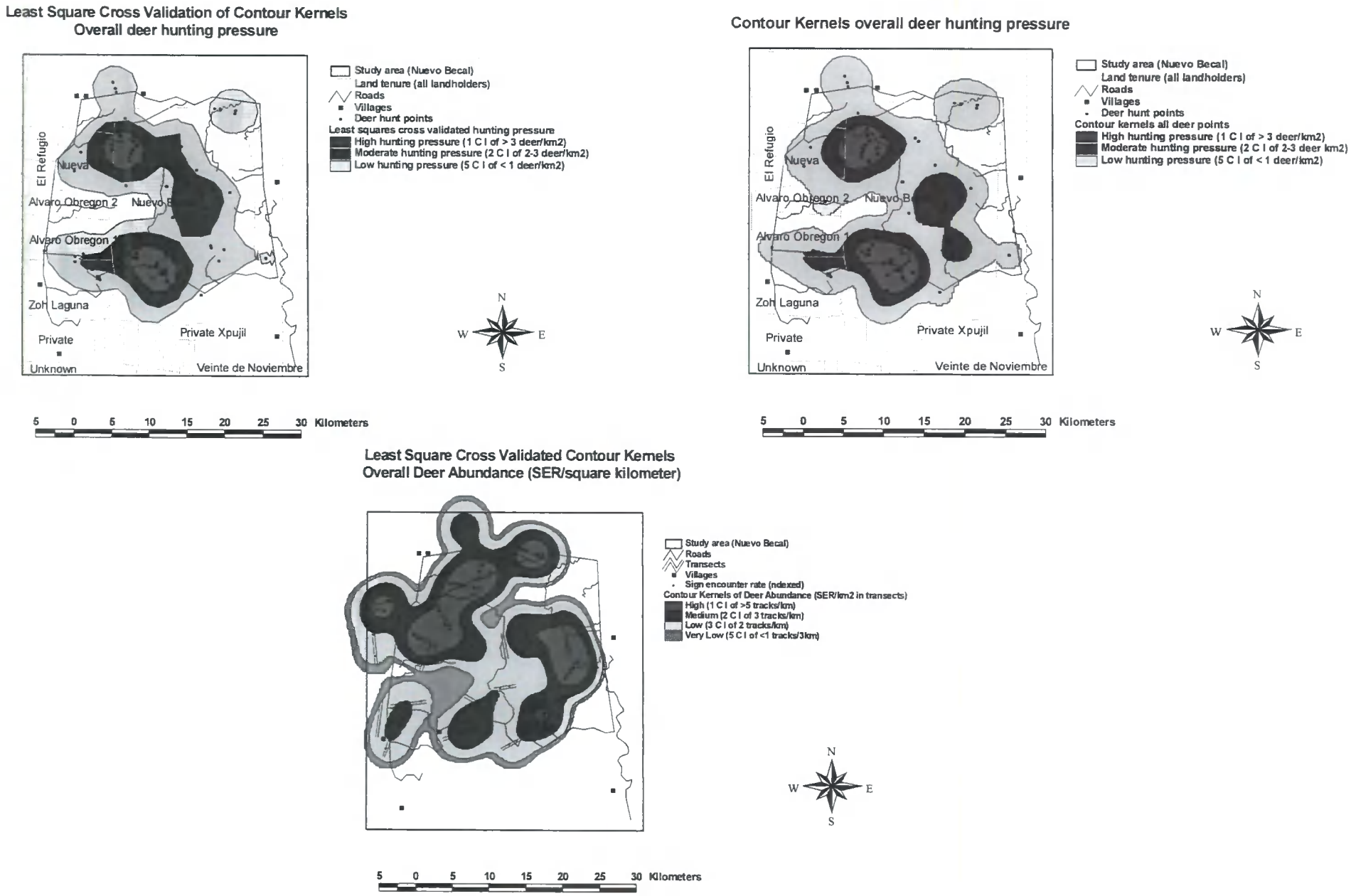

Figure 4.30. Validation of the model for calculating spatial hunting pressure and spatial estimation of deer abundance in the study area, GCR.

4.4. Discussion

4.4.1. Hunting vs. sighting data

The analyses of deer hunting versus sighting data demonstrated that these two sets of observations had fundamental differences in their spatial and temporal arrangement and that sighting data cannot be used indiscriminately to supplement hunting information.
It was clear that hunting information can provide more complete and precise data bases on the species composition, sex and age structure of deer population, than sighting data.
In thick, dense tropical forests, shy mammals such as deer are usually glimpsed (Reid 1997) and when similar species live together, accurate identification of species, sex and age classes can be extremely difficult (Emmons, 1990).

Therefore, the use of sighting information for determination of accurate spatially-explicit deer population parameters in the GCR is very limited. Observations of animals in the wild have been used to determine population parameters of many species of tropical animals (Emmons, 1990; Reid, 1997; Chiarello, 2000) but local conditions such as density of trees, understory and canopy cover can greatly influence the quality and quantity of this observations, and its use for more elaborated models (Carrillo *et al.*, 2000).

4.4.2. Hunting distances to town

The average distance of hunting to the village documented here was slightly larger than that documented in other studies, both in southern Yucatan Peninsula and Peten Region (Jorgenson, 1993, 2000; Morales *quoted in* Escamilla *et al.*, 2000) and elsewhere in the Neotropics (Vickers 1991, Towsend, 1995). This is probably related to the fact that most previous studies documented hunting patterns for a large assemblage of wildlife species rather than only for deer. No other study in tropical forests have concentrated in documenting mean distances from the villages of deer hunters.

Escamilla *et al*, (2000) used a 6 km radius to assess the extent of hunting reach and habitat disturbance in the communities they studied within the GCR. Jorgenson (1993) reported that most hunting occurs within 6 to 12 km from the villages in Quinatan Roo, Mexico and similar distances no greater than 12 km from the villages have been reported for hunters in Ecuador (Vickers, 1991) and Bolivia (Towsend, 1995).

Deer are highly mobile animals with relatively large home-ranges compared with other smaller prey species (Geist, 1998, Kilgo *et al.*, 1998). Deer are also considered a favorite but difficult to hunt prey by many indigenous people (Hurtado-Gonzalez and Bodmer, 2004). The detected mean distances to town reflect this because, they involved much smaller hunting catchments and closer distance to town when hunters where engaged in hunting prey other than deer.

The results suggests that hunters traveled larger distances to town to harvest red brocket deer and shorter distances to hunt white-tailed deer. They also traveled a mean of 600 meters less to hunt juvenile than adult white-tails and brown brockets, but not red brockets. This is suggestive that the availability of juvenile deer of the two former deer species was larger closer to the village than that of the red brocket deer.

Habitat use and feeding patterns of these species may help to explain these differences. While both the white-tailed deer and *M. pandora* behave like habitat generalists (Chapter 2) and consume a wider array of plant resources than *M. americana*, the red brocket is a habitat specialist with a more specialized diet (Chapter 3). The surroundings of the villages are usually more affected by deforestation, clearing for agriculture and provide a richer mosaic for wildlife species in the southern Yucatan Peninsula (Jorgenson 1993, 1995a,b; Escamilla *et al*; 2000). This might be a factor that attract juvenile deer of the two generalist species (*O. virginianus* and *M. pandora*) closer to villages but not the specialist deer (*M. americana*) that find most of its habitat and diet requirements fulfilled within the relatively undisturbed Tall Evergreen forest (Chapters 2 and 3).

4.4.3. Hunting distance to roads

The effect of roads on deer hunting patterns was less clear than the effect of distances to town. This can be indeed a matter of scale and resolution rather than a real biological effect. While distances to town were in the scale of thousands of meters, distances to roads were in the order of hundreds of meters. The margin error of the non-differentially corrected GPS positions plus the margin of error to accurately pinpoint deer killing locations sum up to magnify this situation. However, relatively small standard errors were found and these were within the range of the predicted errors for accurately pinpointing the hunting locations (100 meters radius).

Roads and its effects on deer hunting patterns in this study were also influenced by the large availability of old logging roads in the form of a grid in the Nuevo Becal community (Chapter 1). Therefore, hunters do not heavily depend on the availability of usable roads because they can use old abandoned logging roads as hunting trails or even make their own trails for hunting purposes.

The effects of roads on deer hunting behaviour and vulnerability has been widely documented in temperate forest environments (Kilgo *et al.*, 1998, Lyon and Burcham, 1998; Millspaugh *et al.*, 2000). However, the hunting scenarios in these studies and the present study are totally different. While sport hunters in North America heavily depend on roads for their transport in (often off-road) vehicles to reach hunting grounds and in many cases to move within these hunting grounds, subsistence hunters in Mexico and in most of Latin America usually hunt by foot or those that can afford a bicycle will use one sometimes to transport themselves and their hunted quarry back home (Jorgenson, 1995a, b). Therefore, the availability of roads is probably of minor importance for the estimation of deer hunting pressure in some areas were accessibility by foot to hunting grounds is high. Further studies with higher degrees of accuracy in the determination of both GPS positions and killing locations might be needed to corroborate the possible effect of roads however, because the approach followed in the collection of GPS positions was with a relatively high margin of error within the scale of one hundred meters.

The lack of differences between the estimated straight distances to roads and distances to town and those predicted considered the slope and elevation of the terrain might be explained by the topographic characteristics of the study area. Nuevo Becal and overall most of the study area is located within the Zoh-Laguna Plateau that is characterized by presenting little changes in elevation, slope and topography compared with other areas within the GCR (Turner *et al.*, 2001; Martinez and Galindo-Leal, 2003). The southern Yucatan Peninsula is indeed a very flat region (Turner *et al.*, 2001).

4.4.4. The reach of deer hunting from distances to villages

The potential extent of deer hunting as estimated from the mean and confidence intervals of distances to villages provides a very pessimistic scenario for the conservation of deer

populations and the management of subsistence hunting. According with these results, hunters had potential reach to almost the entire study area and beyond, and to large surface areas within the GCR including large forest tracts in the Calakmul Biosphere Reserve "protected" area.

This hunting reach is potential, however, because it was based in the assumption that hunters in other villages behave in a similar fashion than that of the studied hunters. It seems relatively clear that hunters tend to respect the political boundaries of their land-holdings because only 7 of 60 deer hunting records laid outside the borders of the limits of the Nuevo Becal community (Figure 4.23). If other hunters outside Nuevo Becal also respect these boundaries is unknown, but evidence of encounters with hunters from other communities while doing field work in Nuevo Becal suggests that this is not always true and that hunters from small land-holdings tend to show less respect to political land-holding boundaries than hunters from large land-holdings such as Nuevo Becal (Table 4.7). This was particularly evident when hunters from small land-holdings had easy access to large tracts of forest belonging to large land-holding communities when living just adjacent to these land-holdings (Figure 4.23). During the 5 years of this study, encounters with hunters "poaching" in Nuevo Becal lands and coming from the smaller land-holdings such as of La Mancolona, Alvaro Obregon and even Xpujil (the municipality centre and largest town in the whole GCR) were relatively frequent, specially in areas away from the land owners house-holds.

Neither hunting reach model implies that hunters will be exerting an homogeneous amount of hunting pressure within their hunting reach. Most intensive hunting (as rated by the density of GPS positions) occurred closer to the villages than farther away. This means that hunters are more likely to over-exploit deer populations closer to their villages than away from them and this is a general trend that has been widely documented in other subsistence hunting studies in Latin America and elsewhere (Ayres *et al.*, 1991; Vickers, 1991; Jorgenson, 1993, Alvard, 1995; Bennett and Robinson, 2000; Peres, 2000). Subsistence hunters tend to behave as central place foragers where both prey choice, hunting intensity and other hunting decisions seem to be strongly regulated by the rules of the central foraging theory (Stephens and Krebs, 1986) where resource allocation decisions are linked with the optimisation of benefits to achieve maximum fitness (Vickers, 1991; Alvard, 1993; Robinson and Bennett, 2000). This

hypothesis was confirmed by testing these ideas from a spatially-explicit perspective in hunting behaviour for the first time in a tropical forest. The implications of central place foraging behaviour of hunters will be discussed further in the following sections.

4.4.5. Extent of deer hunting pressure within the villages

Although more qualitative than quantitative in nature, this analyses based on interviews and field notes bring the opportunity to visualize the potential extent of deer hunting from a human community-wide perspective. The hunters that participated in this study were deliberately chosen from the universe of hunters in the GCR among other things because of their hunting experience and willingness to participate in the course of the research for several years. They are rated in their village as some of the best hunters and contribute a sizeable amount of the entire deer hunting harvest each year. These characteristics allowed for the collection of relatively ample information on their deer hunting patterns and other data such as that reported in pervious chapters. This implies however, that this particular sample of hunters might be biased by choosing those hunters that might have exerted one of the heaviest hunting pressures on deer populations within the GCR during the study period. While this might be true at some extent, we were able to estimate how big this bias possibly was by interviewing other members of the hunting community in the study area.

The results suggest that at least another 20 hunters living in the communities immediately surrounding Nuevo Becal may exhibit similar hunting patterns than those surveyed hunters. This is obviously a very rough estimate, because it is impossible to know the accuracy of the information provided during the interviews. However, by living semi-permanently in the study area for a period of more than 5 years with continued communication and good relationships with members of these communities, I believe that the results of these interviews are true or at least very accurate. Thereafter, it can be assumed that the general hunting pressure patterns in the study area are at least two times greater than those exhibited by the nine sampled hunters. This means, for example that instead of 60 deer harvested from 1996-2001 it might had been 180 animals and that instead of a total deer harvest rate of 0.31 deer/km^2/year, it might had been 0.93 deer/km^2/year for the same total catchment area.

Subsistence hunting studies tend to work with samples of hunters rather than with whole human communities, because it is extremely difficult (if not impossible) to obtain the full cooperation of all the people involved. When the scale of the studies is small (e.g. one village, small land-holding size and small study area) it can be possible to attain full community participation on harvest rates, but all previous studies to date have completely ignored the spatial and temporal distribution of hunters and concentrated in documenting lists of total harvest rates (e.g. Vickers, 1991, Jorgenson 1993, Townsend, 1995). While this is very informative on the amount of hunting that a specific community is performing, the specific location on the harvests, accurate catchment areas and proportional off-takes are not possible to obtain. Conversely, when the scale of the study is large (e.g. multiple human communities and multiple land-holding sizes interspersed within a large study area) sampling of hunters becomes mandatory because the human effort and economic costs to obtain complete figures can be prohibitive and it is unlikely to obtain the full cooperation of all the people involved in hunting activities. In these cases, researchers simply extrapolate harvest rates to whole study areas and estimate the likely error with the help of interviews (Bodmer 1994, 1995; Fitzgibbon *et al.*, 1995; Leeuwenberg and Robinson, 2000; Hurtado-Gonzalez and Bodmer, 2004). The spatial and temporal distribution of hunters that attained these harvests, however, has been ignored so far. I argue that this can be a risky practice because it totally disregards the effects of refuges and the potential predator-prey dynamics of hunters and deer moving through the landscape in space and time. The effect of refuges and predator-prey dynamics will be discussed later.

4.4.6. Hunting catchments areas

Two methods were used in this study to assess the size and spatial and temporal arrangement of hunting catchment areas: The Minimum Convex Polygon (MCP) and the Adaptive Kernel (AK) methods. Both methods had advantages and disadvantages for these estimations. While the MCP can be practical and easy to implement to predict the size of the catchments, it tends to overestimate catchment's size by including relatively large areas within the polygons that probably were not used by the hunters. This is related to the geometry and spatial arrangement of the GPS positions where a non-concave polygon will invariably result with this bias (White and Garrot, 1990). Therefore, harvest rates obtained within the MCP-calculated catchments might be underestimated.

On the other hand, the AK method provide a probabilistic approach to this problem where the catchments are divided by probabilities that an specific density of points (e. g. harvest/km^2) will occur within a specific area. This is obviously more appealing than the more simplistic MCP but also has its limitations. A 95% (one confidence interval) probability of occurrence of a high hunting pressure is not the same –in statistical terms- as an 85% probability (three confidence intervals) for a low hunting pressure. The decision was made to set these probabilities in this fashion, firstly; because the highest the density of points, the highest the probability, thus the probability of a high hunting pressure (e. g. largest harvest of deer) and the order of the next two ranks are more or less automatically set by this method (Worton 1989a, 1989b). Secondly, the probability of the next two polygons can be arbitrarily chosen, but with small sample sizes, high probability values should not be set because of the high sensitivity to the variance of the AK method might provide unreliable results if this is ignored (Seaman and Powell, 1996, Mack 2002). This basically means that we can be certain within two confidence intervals, that the calculations of both high and moderate hunting pressures are accurate enough, but the accuracy decreased considerably for the calculation of low hunting pressure.

In other words, this may be translated as if 20% of occasions, hunters might had been harvesting deer at rates lower than 1 deer/km^2 in areas different from those indicated by the probabilistic polygon. Is this margin of error acceptable in biological and management terms? It is difficult to ascertain for sure. For example, 19 of the 60 harvested deer (c. 30%) were hunted in areas of low hunting pressure according with this model. This proportion might set this model as being not very accurate to predict areas with "low" hunting pressure, but accurate enough to predict areas with "high" hunting pressure.

Perhaps more important than the proportions of animals harvested per hunting pressure area, is the size, extent and spatial distribution of the hunting catchment areas in the landscape. This study took place in a relatively large study area (155,000 hectares) where this spatial patterning might have had important implications on the creation of sink and source areas in both space and time for the deer populations (Pulliam, 1988, Pulliam and Dunning 1997; Hansky and Simberloff, 1997). This is apparent from

looking at the differences in the proportion of areas hunted and non-hunted by the participating group of hunters (Table 4.3 and 4.4). I deliberately omitted the low hunting pressure polygons in the analyses of annual catchments to remark these differences in time and space for the two highest probability annual catchment estimates (Figure 4.29). It is clear that large tracts of deer habitat remained unhunted (or at least lightly hunted) by these group of hunters for relatively large periods of time. In any given year, areas equivalent to one third to two thirds of the whole study area remained unhunted and deer populations in these areas might had easily recovered from previous years of exploitation through natural recruitment and immigration, if harvesting by other hunters did not occur or was at least very light. Moreover, some large forest areas potentially within the reach of hunters remained completely unhunted or very lightly hunted during the whole five years study period, potentially functioning as refuge or source areas for deer. This is evident by looking at both the catchment areas calculated by the MCP and AK methods. Many of these areas were found depicting moderate and abundant deer populations through indirect estimations of deer relative abundance (Figure 4.30). Once again the potential function of these non-hunted or slightly hunted areas with apparently healthy deer numbers as refuges for deer populations becomes evident (Figure 4.31)

These results are consistent with the idea of the existence a source-sink system between deer populations and hunters in the study area. Pulliam (1988) and Pulliam and Dunning (1997) defined source sink systems as *"BIDE"* models where high birth (B), high immigration (I), low death (D) and low emigration (E) rates are likely to occur in source areas, whereas the opposite (low birth, low immigration, high mortality and high emigration) will occur in sink areas. The interactions between source and sink areas is dynamic and totally dependent on the performances of these four demographic parameters. While source-sink models are appealing, little empirical evidence exist that they might actually occur in natural settings (Gilpin and Hansky, 1991; Dunning *et al.*, 1992; Doak, 1995, Hansky and Gilpin, 1997, Moilanen *et al.*, 1998) (Figure 4.31).

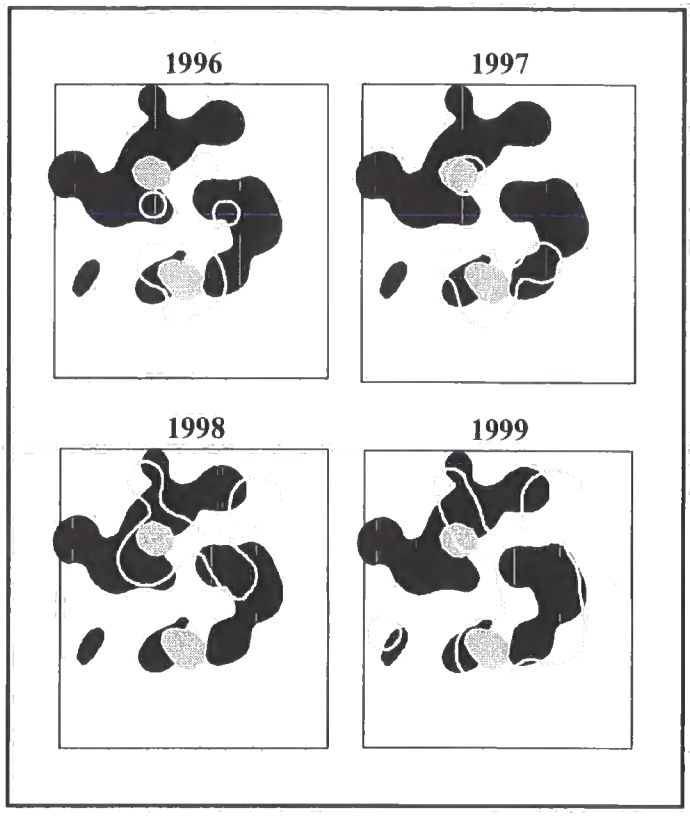

Figure 4.31. The potential role of refuges and the source-sink system between deer populations and hunters in the study area, GCR from 1996 to 1999. The black polygons represent potential permanent source areas where low deer mortality, high juvenile recruitment and emigration were likely to occur (from Figure 4.30) . The grey polygons represent constant sink areas where high mortality by hunting, low juvenile recruitment and immigration-dependence were likely to occur (high hunting pressure areas from Figures 4.28 and 4.29). The line polygons represent the accumulated annual catchments of all hunters for all deer in all age and sex categories where $\geq$ 2 deer/km^2 were harvested (high and moderate annual hunting pressures from Figure 4.27).

4.4.7. Harvest rates and hunting pressure

Compared with other studies in the neotropics, the annualised harvest rates obtained for the *Mazama* species are relatively high (Bodmer, 1995; 1999; Towsend, 1995; Hill *et al.* 1997; Leeuwenberg and Robinson 2000). In a recent study, harvest rates ranging from 0.17 deer/km^2 in heavily hunted areas to 0.06 deer/km^2 in slightly hunted areas were found for *Mazama americana* in the Peruvian Amazon (Hurtado-Gonzalez and Bodmer, 2004). No harvest rates have been published for the white-tailed deer in tropical forests so far.

However, the methods to calculate harvest rates in this study are fundamentally different from those used in other studies, because here harvest rates were direct calculations for "real" catchment areas reflecting space use by hunters rather than extrapolations to whole study areas. Nevertheless, when harvest rates are calculated in a similar fashion to that of previous studies (extrapolating the total harvest to the whole study area) the figures are still higher than those reported elsewhere (Table 4.9). By looking at Table 4.9, it is evident that important hunting records were missed when looking for the collection of GPS deer killing positions. For example, the mean highest hunting pressure shifts from the white-tailed deer to *M. pandora* when all deer records are taken into consideration for the analyses (Table 4.9). It is also evident that overall hunting pressures increase when a 10% error is added to the data base to compensate for possible missing hunting records and the figures are now comparatively similar to those obtained with the MCP and the AK methods to calculate catchment area sizes (Table 4.2 and 4.3).

An important difference between the MCP and the AK methods was found for the white-tailed deer (Tables 4.2 and 4.3). While the MCP provided a comparatively similar harvest rate estimate for the white-tailed deer (0.68 deer/km^2) to that of the two *Mazama* species (*M. americana* = 0.70 deer/km^2 and *M. pandora* = 0.52 deer/km^2), this figure was considerably larger for the white-tailed deer on the high-hunting pressure areas (2.3 against 0.24 and 0.84 deer/km^2, respectively). This is the result of the much higher density of white-tailed deer hunting record points in a relatively small area around the main human settlement (Nuevo Becal) where many white-tails were killed at very close distances from each other. This is interesting, because this area corresponds with one of the major agricultural areas in the village and the result reinforces the finding that white-tailed deer is more attracted than the other two species to agricultural areas as demonstrated in Chapters 2 and 3 and that more deer of this species can be harvested closer to human habitation than the two *Mazama* species. This fact was also demonstrated with a multiple regression analysis for the white-tailed deer (Figure 4.26).

While Hill *et al.*,(1997) and Hill and Padwe (2000) suggested a source-sink model to characterize the hunting patterns of the Aché Indians in Paraguay, their study does not have any spatially-explicit component and therefore the lack of spatially-explicit evidence made this study suggestive rather than empirical in nature. The only other study that has analysed the spatial distribution of hunting pressure in relation with game

vulnerability found similar results to those found in the present study in relation with the tendency to concentrate predation effort around a starting point by human hunters. Broseth and Pedersen (2000) found that the highest hunting pressure on grouse populations in their Norwegian study site was concentrated around the starting point where hunters initiated their hunting trips and that birds closer to the cabin had a higher vulnerability and therefore probability to get killed than birds farther away from the cabin. The authors conclude that studying the spatial distribution of hunting pressure is of paramount importance to understand hunter-prey interactions and the impacts of hunting on wildlife populations. Better sustainability indices can be achieved when spatially-explicit information is incorporated (Milner-Gulland and Akcakaya, 2001).

Other studies have shown that in response to disturbance caused by predators (in this case hunters), individuals on harvested wildlife populations might move to refuge areas where they are inaccessible or more difficult to hunt (Swenson 1982; Naugle *et al.*, 1997; Hill *et al*; 1997, Hill and Padwe, 2000; Novaro *et al.*, 2000, Verkauteren and Hygnstrom 1998; Wiens 1996)

This has enormous implications for the present study because the whole hunter-prey system in the GCR study area might have been functioning as a very dynamic source-sink system (Pulliam 1988; Wiens, 1989) where hunters might have been taking the surplus individuals of the population in some cases and considerable amounts of the standing crop population in others, but the arrangement of both hunters and prey in time and space probably allowed for these areas to remain in a dynamic of depopulation and repopulation with immigrating individuals and new recruitments constantly moving in and out. Evidence for this, has been suggested previously and it is supported by the dynamics in time and space on the use of available terrain exhibited by the hunters and also by the relatively continuous and concentrated harvest of juvenile deer has opposed to the more heterogeneous and spread off-take exerted over adult individuals.

Joshi and Gadgil (1991) and McCullough (1996) argued with theoretical evidence that traditional hunting by indigenous people might be managed by controls on the spatial extent of hunting through the creation of a network of refuges in a matrix of hunted forests. The result of this study and others (Hart 2000) strongly support this idea with

qualified evidence that this might actually be happening by intrinsic mechanisms of unregulated subsistence hunting in the GCR.

4.4.7. Estimated deer abundance spatial indices

The method proposed here for the spatial representation of deer abundance indices is perhaps over-simplistic in the way it was developed and it is obvious that it has several drawbacks. The distribution and abundance of wildlife might be affected by a number of factors that were not taken into consideration by this simple model. Such factors include habitat differences, the effect of disturbance and biases in sampling methodology among many others. Moreover, the model was based in the sampling of transects with large time gaps (e.g. months) between each other that might had influence in the overall distribution of deer in space and time.

However, taken as it is; a simple representation of the relative abundance of deer, it might be informative and useful for comparison with other more traditional and accepted lineal methods presented elsewhere (Chapter 2) and perhaps even more importantly for comparison with the space use by hunters in relation with potential prey availability. By overlaying the maps of hunting pressure and deer abundance (Figure 4.30) its is possible to see that hunters were harvesting deer more or less in relation to prey availability since at least two areas rated as with high hunting pressure laid in areas of high deer relative abundance. Most other hunting areas laid in areas of low and moderate deer relative abundance. Remarkably, the area around the main human settlement that accounted for the highest accumulated hunting pressures in the whole study area, was found as having moderate relative abundance of deer (from 2 to 3 SER /km). This is interesting because it suggests that after at least 5 years (1996-2001) and probably much longer history of heavy hunting pressure in this area, deer can still be found in moderate abundance. The continued and apparently homogeneous deer harvest rates during this period support this finding.

Also of interest, was the finding that a large forest tract in the west of the study area was found has presenting high deer relative abundance indices but it was rarely visited by hunters, with perhaps just one deer harvested by these group of hunters in this area during the five years period. Indirect field evidence suggest that other hunters did not visited this area frequently, in part because accessibility was poor (very bad condition of

roads) and far away from the village. The finding of this non-hunted area with relatively high deer abundance supports the idea of the presence of at least a couple of source areas or refuges within the study area where deer mortality from hunting is low or non-existent and recruitment might be high.

This model also provided a general picture for the overall deer relative abundance in the study area that might be rated as moderate where the probability of finding at least 3 deer SER/km would happen with a 90% probability in at least 25% of the study area. While this technique has been suggested theoretically by some authors (Mack and Quang, 1998, Mack *et al.* 1999, Mack 2002), to the best of my knowledge, this is the first attempt to represent the relative abundance of a tropical wildlife species with the combined use of transect sampling, kernel probabilistic polygons and GIS/GPS technologies.

4.4.8. Overall conclusions

This chapter strongly supports the idea that the deer hunters studied within this particular communities in the GCR behave like typical central foragers, optimising the effort and energy spent in hunting to attain maximum benefit by concentrating this effort around their central living areas (Stephens and Krebs, 1986). This is no new contribution to the knowledge of subsistence hunting (but see review by Redford and Robinson, 1987). What it is probably new, is that this central foraging behaviour is not constant in space and time and that the effort spent in foraging (a. k. a. hunting pressure) is also highly variable both spatially and temporarily. The implications of these variations in human foraging behaviour for the conservation and management of tropical deer populations (and potentially many other species of wildlife) are enormous. These findings highlight and support theoretical arguments presented by others (Joshi and Gadgil, 1991; McCullough, 1996, Walters 2001; Woodroffe and Ginsberg, 1998) with empirical evidence on the importance of refuges (or source areas, Pulliam, 1988) on the dynamics of harvested wildlife populations in tropical forests.

CHAPTER FIVE

General Discussion

5.1. Deer ecology and conservation

It has long been recognized that the management of wildlife populations requires at least a basic understanding of the biology and ecology of the targeted species (Leopold 1977). The more we know about the ecology of a wildlife species, the higher the likelihood of a sustainable management. This fact has been proved again and again with temperate species that have been studied continuously for decades during the past century. Two examples are the red deer (*Cervus elaphus*) in Europe and the white-tailed deer (*Odocoileus virginianus*) in North-America (Clutton-Brock *et al.*, 1982, Waller and Alverson, 1997). These two species have been studied so extensively that are considered by many as two of the better known wild animals on earth (Caughley and Sinclair, 1994).

The history of wildlife management in general (and deer management in particular) can be traced back to the 1920's in some developed countries such as the US and Great Britain. These years of careful and extensive research yielded and enormous amount of knowledge on the ecological requirements of deer in different temperate ecosystems. Deer management, facilitated by this reach knowledge baseline as well as the presence of stable economies, strong law enforcement and lack of human population sectors with subsistence needs, have been so successful that an overabundance of deer populations is the main management problem today (Waller and Alverson, 1997).

The picture in other less developed regions of the world cannot be more contrasting. While some deer species in temperate regions have been some of the most scientifically studied animals on earth, many of their cousins in tropical regions remain as some of the least know mammals in terms of ecological requirements and even basic natural history knowledge (Wemmer, 1998). Moreover, while deer managers in developed regions of the world strive to find solutions to the problem of overabundant deer populations by encouraging sport hunting and researching reproductive contraceptive methods (Waller and Alverson, 1997, Riley *et al.*, 2003) their counterparts in tropical regions such as Latin America and Asia are still discovering new species of deer and desperately trying to document the very basic aspects on the natural history and ecology of others before it

is too late and the "long arm" of the contemporary extinction process may reach them (Aung *et al.*, 2001, Weber and Gonzalez, 2003, Appendix 1).

This thesis is a example of this striking contrast in ecological research between developed and developing countries. It is at least ironic that the first ecological study in one of the recently discovered species of deer; the Yucatan brown brocket deer (*Mazama pandora*), was carried out in both a developing country (Mexico) and a developed country (UK) wit such a contrasting histories in wildlife and natural resource management and conservation. While some argue that the true Naturalists are dying-off in the developed world "degenerating into a generation of technocrats, indoor biologists that see and study nature through computer screens" (Noss, 1996), a new, rejuvenated generation of "new-age" Naturalists is just being born in several developing countries.

This document represent the first attempt north of the Amazon basin of documenting unknown aspects on the natural history and ecology of three sympatric species of tropical deer in one of their largest and most important habitat strongholds in Mesoamerica. In the following sections, the main research findings on these topics will be discussed separately with the ultimate goal of capitalizing on this knowledge for the management and conservation of deer populations in the region. It is clear that one of the factors responsible for this contrasting differences in deer research and management between tropical and temperate regions is the habitat differences in which deer live. Most tropical deer species are solitary forest dwellers living in dense forest thickets that make research difficult, at least. For example the estimation of population densities; one of the most important aspects of the ecology of wildlife populations was restricted in this study to the use of relative abundance indices or inaccurate density estimates based in deer signs and sight counts (Chapter 1). It was impossible to differentiate the signs (e. g., tracks and pathways) of the two *Mazama* species and the number of sightings was so low that density estimations using line transects methods was probably unreliable. However, many other studies have been using and reporting density estimates with these techniques disregarding some of the major assumptions to obtain reliable estimates, such as randomisation and stratification of transects (Escamilla *et al.*, 2000, Hurtado-Gonzalez and Bodmer 2004). While this has not stopped researchers in the past, it is clear that the limitations of these techniques for studies of some tropical forest wildlife are considerable. More research is urgently needed to develop better techniques

for the estimation of deer population densities in tropical forests. One of the most promising methods (albeit an expensive one) is the use of DNA finger-printing for population estimations. This method has been successfully tested for the estimation of bear populations in forested habitats (Wasser *et al.*, 1997). Another possibility is the use of drive counts that has been successfully used for the estimation of forest deer populations in North-America (McCullough, 1982), but the logistics and costs of this method in frontier areas of colonization in Latin America might turn it unlikely.

Notwithstanding the limitations of the techniques for population estimation used in the present study, deer populations in the GCR seem to be relatively stable and no noticeable effect was detected in population trends of the two brocket deer species. Whether one of the *Mazama* sp. is being more affected than the other by human hunting or not is difficult to ascertain, but it seems that the two brocket deer species may accept high levels of human predation with little effect at the population level (Chapter 1). This do not appear to be the case for the white-tailed deer for which a clear decline in abundance was detected, most likely caused by over-hunting.

The results of both the diet and the habitat use studies clearly demonstrate a well demarcated separation among the three species of deer by different ecological niche preferences. The adaptability of the white-tailed deer to live in most habitats and to be favoured by human agricultural activities, evidenced once more the tremendous resilience of this species (Leopold, 1977., Mandujano and Gallina, 1995). However, the fact that two sympatric species of brocket deer are well separated into different ecological niches by presenting different habitat use preferences and different feeding habits is new to the science of tropical wildlife management and conservation in Latin America.

Finding the red brocket deer (*M. americana*) as a well defined habitat specialist was surprising since anecdotal evidence from South America suggested this species as a habitat generalist. One possible explanation for this is that *M. americana* shares its habitat with a number of other deer species in South America including at least another four or five *Mazama* species (Appendix 1), while in Mexico, *M. americana* shares the tropical habitats were it lives only with the white-tailed deer in its whole distributional range and with *M. pandora* in the Yucatan Peninsula (Medellin *et al.*, 1998). It is

hypothesised that these differences in potential competition in South America and Mexico might be responsible for the differentiation as a habitat specialist in Mexico or habitat generalist in South America, although this last statement yet needs to be tested with more scientific research in South America. The contrasting differences in habitat preferences among the three species of deer further complicate the management alternatives for this deer community. While the red brocket deer might need specific habitat management due to its specialized habitat requirements, the brown brocket and the white-tailed deer might benefit from more generalized habitat administration schemes such as the ones currently in vogue for the creation of habitat mosaics with agro-forestry plots.

Another, aspect that needs to be further explored is the use that deer does of seed rain events among certain plant resources. It was found in the present investigation that seed rain is strongly linked and timed with the overall phenological patterns of most of the plants studied. However, no major seed rain events were detected in the phenological plots during the 11 months of continuing monitoring. Instead, a rather even and permanent in-ground availability of ripe, edible fruits was recorded for the three major habitat types studied. It is well known fact by local hunters that deer (and other wildlife) is attracted to certain trees when in fruit bursts and large amounts of ripe fruits become available on the ground. Hunters sometimes take advantage of this situation to hunt deer and pacas (*Agouti paca*) while seating high on the branches of this trees at night and with the help of a hand torch. In fact, this event was recorded a few times in places other than the phenological plots and, if uncommon, seems to be quite regular in some forest patches. This phenomena needs to be explored further because it brings the opportunity for close observations in feeding behaviour of deer and other wildlife species as well as chances for easily trapping *Mazama* deer of an species that otherwise is extremely difficult to find in the thick forest habitats that it inhabits.

The ecological separation in different habitat niches by selective habitat preferences and different feeding habits brings up both challenges and opportunities for the management and conservation of these three species of deer in its shared distributional range in Mexico, Guatemala and Belize. It is clear that in the absence of the strong hunting preferences for the white-tailed deer in the study area, this species would be strongly favoured by the advance of the agricultural frontier.

The creation of a habitat mosaic dominated by mature Tall Evergreen forests favoured the two *Mazama* deer and restricted the advance of the white-tailed deer so far. This is clearly changing today with more and more primary habitat being lost for logging, slash and burn agriculture and the creation of pastures for livestock raising. This has already happened in Costa Rica, probably the only other Central American country with a history in deer research and management (Vaughan and Rodriguez, 1995). However, this same pattern of deforestation would negatively affect the populations of the two brocket deer species, in particular the red brocket deer that depicted strong habitat and dietary preferences for the primary tropical forest.

Another important aspect for the conservation and management of deer populations in the GCR and similar regions in Central America would be the management of the plant species that form the core of the diet of deer in these regions. By far, the two most important components in the diet of the three species of deer (in particular for the specialist red brocket deer) were the Ramon (*Brosimum alicastrum*) and Zapote (*Manilkara zapota*) trees. The fruits of these two species might be considered as the staple foods and keystone dietary elements for the three species of deer. The history of overexploitation of mahogany and cedar in the GCR has set pressures over hard-woods that were considered as undesirable timber in the past (Ericson, 1999, Steadman-Edwards 2001). Until very recently, the cutting of *Manilkara* trees was banned because of the importance for the chewing gum industry. After the collapse of this industry, many Zapotes have been cut for the production of high-quality rail-road sleepers and as exotic hard-wood for the export to European countries. The same has been happening in recent years with the Ramon tree that is sometimes being cut as a cheap soft-wood for human habitation. Without adequate management of these two all important tree species, wildlife populations in general and deer populations in particular would be affected by selective logging. The synergistic effects of slash and burn agriculture, selective logging, periodic hurricanes (that might cause the largest Zapote and Ramon trees to fall off) and occasional wildfires might have an even stronger effect on these two keystone food resources for the regional wildlife.

It is extremely important to document the population status and ecology of the Yucatan brown brocket deer in other parts of its distribution such as the tropical dry forests and

xeric bush-lands and savannas of the northern Yucatan peninsula in order to develop sound conservation and management plans for this endemic species. Further studies in the region should include behavioural approaches to tackle the questions on habitat use, movements and habitat requirements of the two brockets and white-tailed deer. Radio-telemetry studies in tropical forest are potentially difficult and more research is needed to optimise this technique in tropical forest ecosystems. As an example, we spent three years capturing and radio-tagging brocket deer in the GCR with little success in both trapping (only five animals trapped in this period) and the collection of radio-telemetry data. The availability of new automated GPS collars might prove advantageous in some situations, but the closed tree canopy cover of the GCR forest might be an impossible barrier to beat. This research proved that it is feasible to combine advanced techniques (e. g. GIS/GPS) with traditional participatory methods to obtain information on deer habitat use and hunting patterns. This approach deserves much more investigation since its potential as research and management tool is enormous (Conner, 2002; Bussink, 2003).

5.2. Subsistence hunting

The management of subsistence hunting in the GCR is loaded with a number of challenges and opportunities that are yet to be explored as conservation alternatives for deer populations. However, probably the two most important factors to be considered in future management plans are the human population densities and hunting pressure management. These two interrelated factors are probably the single most important issues responsible for the current hunting scenario in the region.

The GCR was almost completely uninhabited by humans for decades after the collapse of the Mayan civilization well into the 20th century (Erickson 1999, Martinez and Galindo-Leal, 2003). The few humans that settled the area in the middle of the 20th century were either temporary settlers during the boom of the natural chewing gum tapping period in the 1940s or scattered permanent logging towns during the 1950s (Steadman-Edwards 2001). Hunting pressure remained low even when the few humans in the area almost certainly relied in wildlife consumption as their main source of animal protein (Escamilla *et al.*, 2000). With the advance of human colonization through the creation of major high-ways dissecting the region from north to south and east to west and the encouragement of the Mexican Federal Government for settling one

of the true last frontiers of colonization in the country, the hunting scenario shifted from one of sustainable wildlife use to one with obvious prospects of unsustainability in the years to come. Hunting pressure increased as the number of human settlements augmented. Some small land-holdings in the south of the GCR in the vicinity of the Calakmul Biosphere Reserve had already extinguished their major game populations and their inhabitants now poach the protected area in search of game (Calakmul Biosphere Reserve head-quarters rangers. Personal Communication 2001).

It has been suggested that the proximity of a hunted area to a protected area increases hunting sustainability allowing the development of source-sink dynamics within wildlife populations (Bodmer, 1995; Hill *et al.*, 1997; Robinson and Bodmer, 1999; Bennett and Robinson, 2000; Novaro *et al.*, 2000). The main hunted area in the present study (Nuevo Becal community) is not adjacent to the Calakmul Biosphere Reserve and does not have the advantage of smaller communities of repopulating of wildlife coming from the adjacent large protected area. Instead, Nuevo Becal is one of the largest land-holds in the region and is this characteristic that allows for the permanence of abundant deer and other wildlife populations. The source-sink dynamics in this case were not related with the proximity of a protected area but rather with elaborated (albeit unintentional) rotation in hunting catchment areas and a large land-holding size.

Some opportunities for wildlife management in the GCR rest in the several large communal land-holdings still presenting large tracts of continuous, relatively undisturbed tropical rain forest. These communities (usually with land-holds bigger than 25,000 ha) are located in strategic positions in the GCR that might favour the movement of wildlife between the large protected area and the smaller communities with evident disadvantages in size and location. To accomplish successful wildlife management programs in these large communities a number of measures need to be implemented including among others human birth control, hunter education and alternative animal protein campaigns as well as the encouragement of temporal and spatial rotation in hunting catchment areas to favour the creation of wildlife refuges.

The spatial and temporal issue regarding the hunting of tropical deer populations ought to be explored further. It was found in this study that the allocation of hunting catchment areas in space and time might favour the creation of sink and source dynamic

areas and refuges for deer populations. This might have been an isolated result of hunting in a large land-holding with a low human population density or a generalized regional hunting pattern in the whole of the GCR resulting from the combination of the habitat mosaic, deer population densities and cultural background of its local inhabitants. If the first hypothesis is true, it would be worth to find ways to promote the rotation of hunting catchment areas in other communities with different characteristics (e.g. smaller land-holdings, different cultural backgrounds). If the second hypothesis happened to be the right one, the prospects of deer and other wildlife management may be greatly enhanced by this unique feature in hunting behaviour and wildlife managers should capitalize on this finding for the management of deer metapopulations.

Apart from the spatial and temporal allocation of hunting catchment areas, another alternative tool for the management of subsistence hunting in the GCR and perhaps in most of other Mesoamerican tropical forests is the proximity of hunted areas to large tracts of wildlife protected habitat. This can be in the form of natural protected areas (such as the Calakmul Biosphere Reserve) or simply by analysing the effect of a large private or communal land-holdings adjacent to several small, usually over-hunted communities. Both scenarios provide the potential for the management of source-sink dynamics in harvested wildlife populations that ought to be studied carefully in the future (Woodroffe and Gisberg, 1998; Bennett and Robinson, 2000). Both protected areas and large land-holding properties adjacent to heavily hunted communities might serve as "source" areas for the "sinks" around them and careful hunting control and monitoring of wildlife populations in these source areas might be the key for successful game management schemes. The GCR brings enormous opportunities in this regard given the large size and shape of the protected area and the availability of several large land-holdings adjacent to the reserve that might function as additional satellite "source" areas. However, while the source and sink model appears to be applicable for deer populations in the GCR, this idea remains to be demonstrated for other game populations, in particular peccaries, paca, armadillos and large birds such as the ocellated turkey and cracids among the most important game species in the region. Further research with these heavily hunted game species is badly needed.

Sustainability can be defined by a very simple equation (albeit one that does not present an optimistic prospect): How much do we consume is the direct result of how many we

are (Ehrlich 1995). The GCR is still one of the strongholds for tropical wildlife in Mexico in part because human consumption of natural resources in the area remained low during the last 100 years or more. Therefore, human consumption has been low because human population densities are one of the lowest in the country: less than 6 people per square kilometre up to 1998 (INEGI 1998). With the swift turn-over in human population numbers in recent years (Chapter 1), management strategies for deer and other wildlife populations need to be experimented rapidly and those demonstrated as successful need to be implemented and monitored periodically as regional policies as a matter of urgency. Adaptive Management (Caughley and Sinclair 1994) of deer and other wildlife populations might be the only viable solution for the many pressures that the explosion of human populations will bring to the natural protected area in particular and the GCR in general.

Rangers, local wildlife managers, extension workers and postgraduate students ought to be continuously trained as the discovery of new ecological knowledge take place and gets up-dated. Since 1995 the number of both national and international scientific institutions working in the GCR has been steady or even increasing, but the wealth of knowledge generated by ecological researchers working on the natural resources of the region and obtained in the past ten years has not yet been successfully applied with management purposes. To overcome this, a shift from basic ecological research to a new management-driven paradigm is necessary and careful integrative research approaches (e. g. incorporating ecological, anthropological and socio-economical research) must be followed.

5.3. Habitat ecology and conservation

One of the most disregarded topics of applied ecology in tropical forest ecosystems has been the field of habitat ecology for the purpose of wildlife management (Frumhoff, 1995). While considerable research effort is been invested in habitat restoration and conservation of degraded habitats (Caughley and Sinclair 1994), very little research has been carried out on how the structure, composition and function of wildlife habitats can be used for the management of wildlife populations. With this regard, this thesis provided the first comprehensive quantitative phenological study of some of the most important plant species for herbivorous wildlife (including deer) in the GCR. This information provided some insight on how the ecology of different forest classes

preferred by deer might be used for the management of deer populations. For example, the potentially stressful feeding period that takes place in the GCR during the dry season within the Tall evergreen forest and the apparent compensatory fruit production within the mixed Lowland flooding forest suggested a dynamic relationship that might involve local or even regional animal movements between these two habitat classes (Chapter 3). This has been suggested as an explanation for the local "migration" of literarily thousands of parrots in search of better feeding grounds into different forest classes (Martinez and Galindo-Leal, 2003). Taking advantage of this new knowledge might help improve, for example, the likelihood for trapping success of deer and other wildlife species for research purposes, if population aggregations similar to those reported for the parrots take place in a similar fashion during the periods of fruit scarcity.

As mentioned earlier, the management of keystone plant resources for deer and other wildlife might open the possibility for a new and exciting field in the science of tropical applied ecology in the region. Highly seasonal forests such as those found in the GCR might be much more feasible for habitat restoration and management than non-seasonal tropical rain forests (Terborgh 1974, VanSchaik *et al.*, 1993). This is because seasonality itself brings about several unique opportunities such as the one mentioned above. Several reforestation campaigns have been taking place in the CGR for the past five years. Most of the efforts of reforestation had taken place with precious wood species such as broad-leaf mahogany and cedar in an attempt to re-establish this over-exploited species (Erickson 1999, Martinez and Galindo-Leal, 2003). It has been suggested that the current distribution of *Brosimum alicastrum* (Ramon trees) might be the result of intensive management by the ancient Mayas, since it is well know that this tree was widely utilized by this ancient civilization (Martinez and Galindo-Leal, 2003).

The potential for reforestation with keystone plant resources such as Ramon, Zapote and other trees must be explored, perhaps in pilot studies with degraded habitats (restoration plots) or in agro-forestry plots currently in vogue among several Integrated Conservation and Development Projects (ICDP) within the GCR. The benefits of reforesting with highly productive fruit trees such as the ones mentioned above can be many, but perhaps the most important would be increasing the available food supply for many game species including deer, peccaries and agouties as well as non-game species such as tapir, monkeys and hundreds of bird species (Naughton-Treves, 2002).

Perhaps the most challenging of all the possible scenarios for wildlife habitat management would be dealing with the current rates of deforestation for slash and burn agriculture and the modification of the habitat mosaic available for wildlife (Frumhoff, 1995, Robinson and Bodmer,1999). It has been suggested that the creation of this heterogeneous habitat mosaic is in part responsible for the rich diversity and abundance of wildlife resources in the region (Jorgenson 1993, 1995a, b; Escamilla *et al.,* 2000). However, current rates of deforestation are accelerating and more and more habitat is been transformed for agricultural or livestock fields (Trejo and Dirzo, 2000). This will need both immediate action on behalf of the authorities to reverse this process and intelligent reforestation and restoration campaigns to help restore spoiled habitats as well as protection of key habitat elements such as "Ramonales" (clusters of Ramon trees) as keystone habitat resources for wildlife. Finally, keeping a habitat mosaic where the dominant vegetation class would be the relatively undisturbed "primary" tropical forest (and here by "primary forest" I mean continuous forest tracts or patches connected by corridors of at least 30 years of age without major clear-cutting logging operations) and regulating subsistence hunting by keeping human densities at relatively low levels (say, current 1-6 humans/km^2) might be the key to ensure the permanence of healthy wildlife populations in years to come.

The Greater Calakmul Region is a magical place in the centre of one of the last continuous tropical forests north of the Amazon: The Mayan jungle. This place represents one of the last hopes for the long term conservation of regional natural resources. The huge developmental pressures that this area will be experiencing in the next 10 or 20 years will dictate the success of current conservation models in the area, such as the Calakmul Biosphere Reserve and other protected areas (Trejo and Dirzo, 2000). It is clear that these traditional conservation models have been insufficient and new creative approaches outside protected areas ought to be explored. The conservation of deer and other wildlife populations in the Mayan jungle requires careful ecological research, development of creative habitat management alternatives and monitoring of both wildlife populations and hunting activities, but most importantly, it will require political will and creative conservation thinking. Failing to achieve this, will invariably result in just another conservation failure that the world simply can no longer afford.

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Appendix I

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Latin American deer diversity and conservation: A review of status and distribution[1]

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Abstract: We reviewed the scientific literature published from 1940 to 2002 on Latin American (Mexican and Central and South American) deer (Mammalia: Cervidae), focusing on conservation status and prediction of geographic distributions. The extant Latin American deer are the most diverse deer assemblage in the world (Cervinae: one genus, one species: Elk [*Cervus elaphus*]; Odocoilineae: six genera, 18 species: White-tailed deer [*Odocoileus virginianus*], mule deer [*O. hemionus*], marsh deer [*Blastocerus dochotomus*], pampas deer [*Ozotoceros bezoarticus*], huemul [*Hippocamelus bisulcus*], taruca [*Hippocamelus antisensis*], greater pudu [*Pudu mephistophiles*], lesser pudu [*Pudu pudu*], and six recognized species of brocket deer [*Mazama americana*, *M. gouazoubira*, *M. nana*, *M. bricenni*, *M. chunyi*, and *M. rufina*] as well as three recently proposed species [*M. pandora*, *M. rondoni*, and *M. bororo*]). Within this group, three genera (*Odocoileus*, *Hippocamelus*, and *Blastocerus*) have been well studied, whereas the genus *Mazama*, *P. puda*, *P. mephistophiles*, and *H. antisensis* have received little attention. The marsh deer, pampas deer, taruca, huemul, lesser pudu, and two *Mazama* species (*Mazama nana* and *M. bororo*) are the most endangered species. They are each listed as Convention International for the Trade of Endangered Species Appendix I and are considered by the International Union for Nature Conservation to be near threatened or endangered. We updated or created distribution maps for these species. Current research predominantly centres on easily available species (*e.g.*, white-tailed deer in Mexico) or endangered species (*e.g.*, marsh deer in Brazil). In contrast, the ecology and conservation status of the pudu, taruca, and *Mazama* sp. remain largely unknown.
Keywords: conservation, deer, distribution, Latin America, neotropics.

Résumé : Nous avons procédé à une revue de la littérature scientifique publiée entre 1940 et 2002 et traitant des Cervidae (Mammalia) de l'Amérique latine (Mexique, Amérique centrale et Amérique du Sud). Nous avons concentré nos recherches sur l'état des populations et sur les méthodes de prédiction des répartitions géogaphiques. Les cervidés de l'Amérique latine constituent l'assemblage de cerfs le plus diversifié au monde (Cervinae: un genre, une espèce : le wapiti (*Cervus elaphus*); Odocoilineae : six genres, 18 espèces : le cerf de Virginie (*Odocoileus virginianus*), le cerf mulet (*O. hemionus*), le cerf des marais (*Blastocerus dichotomus*), le cerf des pampas (*Ozotoceros bezoarticus*), l'huemul (*Hippocamelus bisulcus*), le cerf andin ou guemal (*Hippocamelus antisensis*), le pudu du Nord (*Pudu mephistophiles*), le pudu du Sud (*Pudu pudu*) et six espèces reconnues de mazamas ou daguets (*Mazama americana*, *M. gouazoubira*, *M. nana*, *M. bricenni*, *M. chunyi* et *M. rufina*) ainsi que trois autres espèces récemment proposées (*M. pandora*, *M. rondoni* et *M. bororo*). À l'intérieur de ce groupe, trois genres (*Odocoileus*, *Hippocamelus* et *Blastocerus*) ont été bien étudiés. Par contre le genre *Mazama*, de même que *P. puda*, *P. mephistophiles* et *H. antisensis* n'ont fait l'objet que de peu d'attention. Le cerf des marais, le cerf des pampas, le guemal, l'huemul, le pudu du Sud et deux espèces de mazama (*Mazama nana* et *M. bororo*) sont toutes des espèces en danger de disparition. Elles figurent dans l'Annexe 1 de la Convention sur le commerce international des espèces de faune et de flore sauvages menacées d'extinction et elles sont considérées comme menacées ou en danger de disparition par l'Union internationale pour la conservation de la nature (Union international pour la conservation de la nature). Nous avons mis à jour ou établi les cartes de répartition de ces espèces. Les recherches en cours s'intéressent essentiellement aux espèces facilement accessibles, comme le cerf de Virginie au Mexique, ou aux espèces en danger de disparition, comme le cerf des marais au Brésil. En contrepartie, l'écologie et le statut des populations du pudu, du guemal et des espèces de mazama demeurent bien peu connus.
Mots-clés : Amérique latine, cerf, conservation, répartition, zone néotropicale.

Nomenclature: Wilson & Reeder, 1993.

Introduction

Latin America is one of the most biologically rich regions in the world. It harbours three of the so-called "mega-diversity" countries and has the largest deer diversity in the world, with seven genera and 18 species described to date (Medellin & Ceballos, 1994; Wemmer, 1998.)

In North America (including Mexico) contemporary deer population depletion commenced during the 18th century with the introduction of modern weapons. Most will agree that indigenous hunting had minimal impact upon deer number before European settlement. However, some argue that at least part of the megafauna extinction process in South America (including that of deer) started much earlier during the Pleistocene and was strongly linked with indigenous human hunting (Eisenberg,

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1987; 1989; Redford & Eisenberg, 1989; Robinson & Bennett, 1999).

Deer biology studies began in Brazil in the early 1900s with Goeldi (1902) and de Miranda Ribeiro (1919), while in the 1940s studies extended elsewhere in South America (Cabrera, 1943; 1960; Cabrera & Yepes, 1961). In the late 1950s, deer research extended to Mexico (Leopold, 1959). Central America (with the possible exception of Costa Rica) has not yet had a local school of deer biologists (Mendez, 1984; Vaughan & Rodriguez, 1994).

Most studies on Latin American deer to date have concentrated on gathering only baseline information. For example, from 1975 to 1995 diet studies and population survey methodology formed the core of deer research in Mexico (Galindo-Leal & Weber, 1998). For some species, even gross geographical range maps are lacking, and no previous literature review has attempted to produce them. In fact, the last literature review is now 5 y old and was not comprehensive, due to the difficulty of obtaining the literature and first-hand information in the region (Wemmer, 1998).

Our aims with this review were to compile the available biological information on deer; update the distribution maps of the species, focusing on their geographic ranges and main populations; and discuss the conservation status and research trends of the 18 Latin American deer species described to date.

Methods

We reviewed the available literature, including that published locally or nationally from 1940 to 2002 in the form of books, proceedings, dissertations, theses, project reports, and memoirs of workshops and meetings. Such sources were often hard to locate in such a large area as Latin America, so in many cases we contacted authors or people involved with ongoing research. Therefore, though we try to keep these to a minimum level, several personal communications are quoted. We divided the continent into three major geographical regions (Mexico, Central America, and South America) and evaluated the information on a species by species basis.

A major aim of our work was to update (or, for some species, create for the first time) distribution maps of the 18 species of Latin American deer. To accomplish this, we followed the International Union for the Conservation of Nature - Species Survival Commision (IUCN-SSC) criteria for extent of occurrence and area of occupancy (Wemmer, 1998), using published information and museum records for historical distribution maps. For predicted and current distribution maps, we used published and unpublished information (so-called grey literature) and personal communications with local and regional experts. We also developed potential distribution maps based on regional habitat. We used ArcView®GIS and the World Wildlife Fund World Eco-Region maps at continental and country scales. Based on available data of the presence of a species in a given habitat and expert knowledge on the extent of this habitat at regional levels, we predicted and/or updated the distribution maps accordingly.

Given the lack of knowledge about many deer species, we focused on documenting current levels of disturbance (*e.g.*, deforestation and overgrazing) of the different habitats, basing our predictions on deer distribution largely on estimations of suitable habitat extent. Clearly, at such large scales, accuracy is compromised, and therefore our maps should be considered to depict potential distribution rather than actual distribution. However, for many species, this is the first attempt to put together this information and to predict gross distributions. Finally, we predicted generalized regional deer diversity patterns (species richness) based on our potential regional distributions maps.

Results

The current conservation status (Convention on the International Trade of Endangered Species [CITES]), geographic range, habitat, and some biological parameters of the 18 species of deer currently known to science in Latin America are summarized in Table I. In the following sections, we provide a species-by-species account and then discuss some deer diversity patterns and research trends by region. Given the lack of consensus on deer subspecies, we keep our discussion at this taxonomic level to the minimum. Distribution maps of the 18 species are summarized in Figures 1-4. Individual maps for each species can be obtained by contacting the authors.

SPECIES ACCOUNTS

WAPITI (CERVUS ELAPHUS NELSONI)

As a result of over-hunting, the Mexican subspecies of elk (*C. e. merriami*) became extinct in the early 1920s in the U.S.A. and Mexico (Leopold, 1959). It once roamed from southern New Mexico and Arizona to northern Sonora, Chihuahua, and Coahuila states in Mexico (Leopold, 1959), having spread from a very restricted original distribution in the oak-pine forests of the Sierra Madre of Mexico. The Rocky Mountain subspecies (*C. e. nelsoni*) has since been reintroduced at private properties in Sonora, Coahuila, Chihuahua, and Durango in northern Mexico (Weber & Galindo-Leal, in press). This is not to be confused with the European red deer (*C. e. scooticus*) introduced for deer farming in several Latin American countries, such as Argentina, Chile, Uruguay, and more recently Mexico (Figure 1). The outlook for this species is difficult to assess since the few remaining herds are all in private properties belonging to wealthy ranchers.

MULE DEER (ODOCOILEUS HEMIONUS)

The distribution of the mule deer in Latin America is restricted to northern Mexico, where there has been an estimated 60% reduction in the historic distribution (Figure 1). It is now well managed for sport hunting in some private properties in Sonora and Chihuahua, Mexico (Weber & Galindo-Leal, in press).

Five subspecies of mule deer are recognized in Mexico: *O. h. cerrocensis*, *O. h. crooki* (syn. *O. h. ermicus*), *O. h. fuliginatus*, *O. h. peninsulae*, and *O. h. sheldoni* (Hall, 1981). Most research has been carried out with three subspecies (*O. h. crooki*, *O.h. peninsulae*, and

TABLE I. Summary information of the 18 species of Latin American deer.

Species (common name)	Geographic range	Habitat (Considered to predict distributions)	Body size & feeding habits	IUCN-CITES conservation status
Blastocerus dichotomus (Marsh deer)	Argentina, Bolivia, Brazil, Paraguay, Peru, Uruguay†	Marshes and wet savannas with high grass and wooded island, damp forest edges	100-150 kg Browser	Vulnerable VU A4acde CITES I
Cervus elaphus merriami (Wapiti, elk)	Mexico†	Forest lowlands and mountains	75-340 kg Grazer & browser	Extinct (reintroduced)
Hippocamelus antisensis (Taruca)	Argentina, Bolivia, Chile, Ecuador†, Peru	Open Andean grasslands	45-65 kg Grazer	Data deficient-CITES I
Hippocamelus bisulcus (Huemul)	Argentina, Chile	Mountain forest dense shrub	45-65 kg Grazer & browser	Endangered EN C2a -CITES I
Mazama americana (Red brocket)	Mexico, Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, Panama, Ecuador, Colombia, Venezuela, Trinidad, Guyana, Suriname, French Guyana, Brazil, Argentina, Bolivia, Paraguay, Peru	Tropical forest and woodlands, cloud forest, and cerrado	30-40 kg Browser & frugivore	Data deficient DD
Mazama bororo (Small red brocket deer or Brazilian Atlantic forest deer)	Brazil	Atlantic forest Brazil	25 kg	Data deficient DD
Mazama bricenni (Dwarf grey brocket)	Venezuela	Mountain cloud forest	Unknown	Not included
Mazama chunyi (Peruvian dwarf brocket)	Bolivia, Peru	Humid forest yungas	> 14 kg	Data deficient DD
Mazama gouazoubira (Grey or brown brocket)	Ecuador, Colombia, Venezuela, Trinidad, Guyana, Suriname, French Guyana, Brazil, Argentina, Uruguay, Peru, Bolivia	Forest, woodlands, dry deciduous forest, or savannas cerrado	20-30 kg Browser & frugivore	Data deficient DD
Mazama nana (Brazilian dwarf brocket)	Argentina, Brazil, Paraguay	Tropical rain forest	10-13 kg	Data deficient DD
Mazama pandora (Yucatan brown brocket)	Mexico	Tropical semi-deciduous and tropical flooding forests	15-20 kg Browser & frugivore	Data deficient DD
Mazama rondoni (Small gray brocket)	Brazil	Amazonian rain forest	15 kg	Not included
Mazama rufina (Colombian dwarf brocket)	Ecuador, Colombia	Mountain forest 3000-4000 m	15 kg	Lower risk-least concern
Odocoileus hemionus (Mule deer)	Mexico	Forest mountains, plains, and deserts	100-120 kg	Lower risk-least concern
Odocoileus virginianus (White-tailed deer)	Mexico, Coiba I, Panama, Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, Panama, Margarita I, Venezuela, Curaçao, Colombia, Eucador, French Guiana, Guyana, Peru, Suriname, Venezuela, Brazil	Forest, woodlands, edge/ shrub, and open grassland	40-60 kg Grazer & browser	Not listed
Ozotoceros bezoarticus (Pampas deer)	Argentina, Bolivia, Brazil, Paraguay, Uruguay	Pampas, open grassland, and cerrado	20-40 kg Grazer & browser	Near threatened NT CITES I
Pudu mephistophiles (Northern pudu)	Colombia, Ecuador, Peru	Temperate forest and fringing grasslands 2000-4000 m	5.8-13 kg Grazer & browser	Lower risk-near threatened-CITES II
Pudu puda (Southern pudu)	Chile, Argentina	Humid *Notofagus* forest up to 1700 m	5.8-12 kg Browser	Vulnerable VU A1cde -CITES I

† Locally extinct.

O. h. cerrosensis, in that order) with little research effort focusing on the remaining two (Galindo-Leal, 1993; Weber & Galindo-Leal, in press). The status and future of the Tiburon Island mule deer (*O. h. sheldoni*) seems secure because of the isolation of the island and its well-protected status as a Nature Reserve. The Cedros Island mule deer is probably the most endangered subspecies (Figure 1).

WHITE-TAILED DEER (ODOCOILEUS VIRGINIANUS)

The white-tailed deer is by far the most extensively studied deer species in Latin America, particularly in Mexico, and it is also of the most polytypic, with around 20 subspecies described for the region (Folliot & Gallina, 1981; Vaughan & Rodriguez, 1994; Galindo-Leal & Weber, 1998). Most research work has been obtained on five to six subspecies, mostly from northern Mexico and

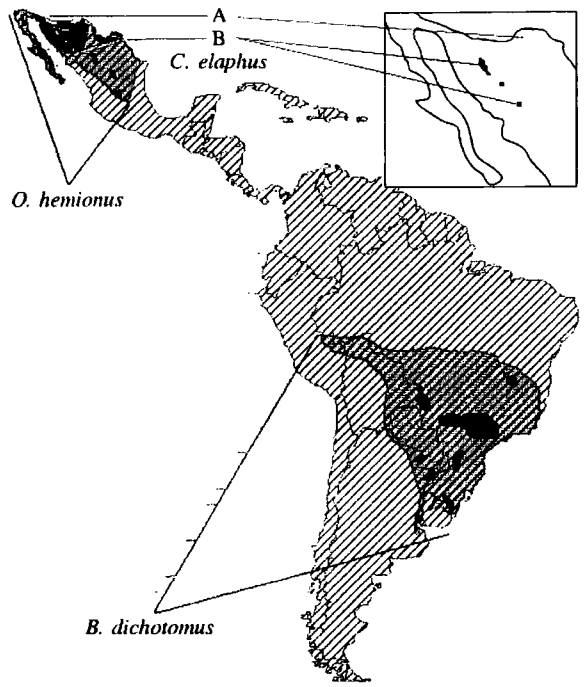

FIGURE 1. Historic distribution (grey) and predicted current distribution (black) of *Cervus elaphus*, *Odocoileus hemionus*, and *Blastoceros dichotomus* in Latin America. The inset zooms on *C. elaphus* (A) historic and (B) predicted distributions in Northern Mexico.

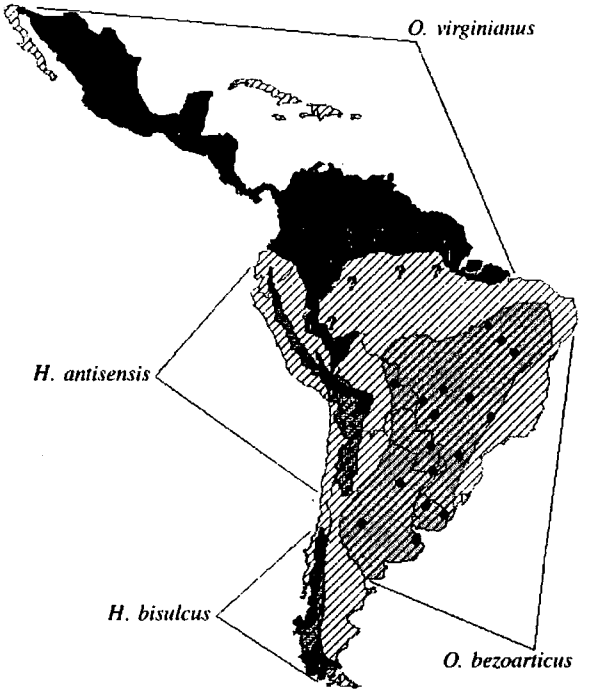

FIGURE 2. Historic distribution (grey) and predicted current distribution (black) of *Odocoileus virginianus*, *Hippocamelus antisensis*, *H. bisulcus*, and *Ozotocerus bezoarticus* in Latin America. Note that only current distribution is given for the white-tailed deer with possible range expansions pointed with question marks.

Costa Rica (Vaughan & Rodriguez, 1994; Weber & Galindo-Leal, 1994). Local extinctions due to over-hunting are common where it is one of the most sought-after game species (Figure 2). Although formal research on the white-tailed deer in Mexico started in the 1980s and has continued uninterrupted since then, most work has been carried out in just three or four states in the north of Mexico (Durango, Nuevo Leon, Chihuahua, and Jalisco), encompassing two or three subspecies that inhabit semi-arid shrub-land and/or oak-pine habitats. Until recently, deer biologists in Mexico have largely ignored the tropical subspecies of white-tailed deer (with the notable exceptions of Chamela tropical dry forest biological station, Jalisco, Mexico [Mandujano & Gallina, 1995] and the tropical rain forest of Calakmul, Campeche [Weber & Reyna-Hurtado, 1999]).

Of the 14 subspecies described in Mexico, research and conservation status evaluations have been carried out for about seven to eight races, with major gaps in the distribution and current status of the tropical (*O. v. oaxaquensis*, *O. thomasi*, *O. truei*) and western Pacific coast (*O. v. sinaloae*, *O. v. acapulcesis*, *O. v. oaxaquensis*) subspecies. Most ecological research has been carried out on three subspecies: the Coues deer (*O. v. couesi*), the Texas deer (*O.v. texanus*), and the Potosi white-tailed (*O.v. miquihuanensis*) (Weber & Galindo-Leal, 1994).

In central America, most research on white-tailed deer has been carried out in Costa Rica (Vaughan & Rodriguez, 1994), where it is one of the most important trophies for sport hunters, resulting in considerable effort being spent on managing the remaining populations (Vaughan & Rodriguez, 1994).

In contrast with Mexico and Central America, where the white-tailed deer has been relatively well studied, the South American subspecies have been largely ignored. The only notable exceptions are in Venezuela (Brooks, 1984) and in Suriname (Branan & Marchinton, 1985; Branan *et al.*, 1985). A recent paper (Molina & Molinari, 1999) proposed that Venezuelan and other Neotropical *Odocoileus* are not conspecific with *O. virginianus* and should be considered different species. Since this work was based on morphometrics, more studies using modern molecular genetics techniques are needed to test this proposal.

The species range seems to be expanding in the south as a result of deforestation, with some recent records of the species in Bolivia, Peru, and Brazil, where it was previously unknown.

MARSH DEER (BLASTOCERUS DICHOTOMUS)

The marsh deer is the largest neotropical cervid with morphological and ecological adaptations to wetlands and riparian habitats (Pinder, 1996; Wemmer, 1998). It was originally distributed in most riparian marshlands from south of the Amazon River to northern Argentina (Pinder, 1996; Tomas, Beccaceci & Pinder, 1997), though we now estimate a 65% reduction in its global distribution (Figure 1).

Total population numbers are unknown, but are certainly declining in all areas as a result of poaching, cattle diseases, habitat loss due to agricultural activities, and dam construction (Beccaceci, 1994; Pinder & Seal, 1994; Duarte, 2001). In Uruguay it is probably extinct since the last record is from 1958 (González, 1994).

The population of the Brazilian Paraná basin is losing habitat for the species at an alarming rate due to the many dams that were built recently (Duarte, 2001). The Argentinian Iberá population is estimated to be 1,000 individuals inhabiting 12,000 km^2 (Beccaceci, 1994). The central part of Iberá consists of swamps and shallow lagoons less than 5 m deep. Most of the basin is at least periodically flooded. The Iberá is the second largest wetland in South America (Pinder & Grosse, 1991).

The other Argentinian population is Delta Paraná, the southern population located at south of the Paraná in the Delta. This population is being affected by habitat fragmentation due to forestation with exotic tree species and poaching (Varela *et al.*, 2001). The estimated population is around 300 to 400 individuals in total (D. Varela, pers. comm.).

The marsh deer is an important component for several new eco-tourism enterprises in the Pantanal region, Brazil, though elsewhere development projects in the form of dams (especially in the Parana-Paraguay river basins) are a major threat to the conservation of several of the remaining habitat strongholds of the species (Beccaceci & Merino, 1994; Beccaceci, 1996; Pinder, 1996; Duarte, 2001).

Over the last 20 y, there has been considerable research in the form of population surveys and captive breeding (Tomas, Beccaceci & Pinder, 1997). Studies on marsh deer include population estimates using aerial censuses (Schaller & Vasconcelos, 1978; Beccaceci & Merino, 1994; Beccaceci, 1996; Pinder, 1996; Mourao *et al.*, 2000; Duarte, 2001) and studies of diet and foraging behaviour (Beccaceci & Merino, 1994; Beccaceci, 1996; Tomas & Salis, 2000), reproductive biology (Duarte, 1992; 2001), genetics (Duarte, 1992; González *et al.*, 2001), diseases (Duarte *et al.*, 2001), home range, activity patterns and captive breeding (Schaller & Vasconcelos, 1978; Duarte & Merino,1997; Duarte, 2001).

In 1994 a Population and Habitat Viability Analysis (PHVA) workshop was held, and the viability trends of the main population from Brazil were analyzed. The analysis showed that the Sao Paulo population would decline at an alarming rate. Captive populations had a high mortality rate. Many of the PHVA recommendations were implemented in Brazil. It is important to analyze the population trends in the current conditions (Pinder & Seal, 1994).

Pampas deer (Ozotoceros bezoarticus)

The pampas deer formerly occupied a range of open habitats such as grassland, pampas, savanna, and cerrado (Brazil). However, the area encompassed by these habitats has been dramatically reduced to less than 1% of that present in the 1900s (González, 1994; 1999).

The largest extant populations from *O. b. bezoarticus* are found in Brazil in the northeast cerrado ecosystem, where about 2,000 individuals live, and in the Pantanal region. Merino *et al.* (1997) estimated an available area of 125,116 km^2 that could potentially support 20,000 to 40,000 individuals (Figure 2).

In Argentina at the turn of the century over 500,000 km^2 of grassland habitat was available, and pampas deer populations were likely very large (González, 1999). However, due to an increase in agricultural activities, today only two small populations remain.

In Uruguay, two remaining populations were described as two new subspecies (González, Álvarez & Maldonado, 2002). One of the subspecies, *O. b. arerunguaensis*, is located mainly in Salto Department, inhabiting an area of less than 120 km^2 with a population numbering fewer than 500 mature individuals (González, 1999). The other subspecies, *O. b. uruguayensis*, is located in Rocha Department, inhabiting an estimated 15 to 20 km^2 with an estimated 300 individuals.

With an estimated 98% reduction in historic distribution, the pampas deer is perhaps the most endangered tropical Latin American deer (González *et al.*, 1998). The main reasons for the fragmentation of the pampas deer population are extensive land use for cattle and agriculture (soy beans, sugar cane) and forestry projects such as the exploitation of pine and eucalyptus plantations (González, 1997; Merino *et al.*, 1997; González, Álvarez & Maldonado, 2002). Population trends from Uruguay and Argentina were analyzed in a PHVA workshop (González *et al.*, 1994). The small populations showed a high risk of extinction. As a result, considerable research is being invested in the study of pampas deer biology, ecology, and conservation in the fragmented populations of Uruguay, Argentina, and Brazil (Jackson, Landa & Langguth, 1980; Jackson, 1986; 1987; Jackson & Langguth, 1987; Jackson & Giuletti, 1988; Leeuwenberg *et al.*, 1997; Gonzalez *et al.*, 1998; Mathias, Girio & Duarte, 1999; Rodriguez & Monteiro-Filho, 2000; González, Álvarez & Maldonado, 2002).

The Andean deer

Taruca (Hippocamelus antisensis)

The taruca is by far the least known of the Latin American deer species and one of the least understood deer species globally. Though local extinctions as a result of over-hunting are common in the Peruvian and Bolivian Andes (Iriarte, Feinsinger & Jaksic, 1997; Regidor & Rosati, 2001), the taruca seems to persist in highly disturbed areas (H. Zevallos, pers. comm.). It has experienced at least a 60% reduction in global range (Figure 2). Its biology and ecology are poorly documented. A handful of reports on the distribution and social behaviour of this species have been published (Roe & Rees, 1976; Regidor & Rosati, 2001), but little is known about its ecology, reproductive biology, or any other biological aspect in the wild. Captive breeding is difficult, and the few attempts have proved unsuccessful (Redford & Eisenberg, 1989; Wemmer, 1998).

Huemul or Patagonian deer (Hippocamelus bisulcus)

The range of this species has contracted greatly, owing to habitat destruction for agriculture and cattle grazing (Iriarte & Jaksic, 1986; Diaz, 1993; Frid, 2001). We estimated at least a 70% reduction in its overall distribution, and this estimate is similar to estimates by local experts (Diaz & Smith-Flueck, 2000). At present, only a handful of protected areas in Argentina and Chile contain herds, and the species is practically extinct outside of these areas (Figure 2).

The social and foraging behaviour, reproduction, and distribution of these deer are well documented, with a number of studies carried out in Chile (Povilitis, 1983; 1984; 1998; Frid, 1994; 1999; 2001) but just a handful in Argentina (Smith-Flueck & Flueck, 1987; Serret, 2001). It is the national animal of Chile, where it has been actively protected for many years. The current bi-national protection agreement between Argentina and Chile is important in assisting the implementation of conservation measures (Serret, 2001).

NORTHERN PUDU (PUDU MEPHISTOPHILES)

Together with the taruca and some *Mazama* species, the northern pudu is one of the most poorly known mammals on the continent. The biology of the species is practically unknown, though it may be a habitat specialist (Eisenberg, 1989). It has been reported as highly susceptible to predation from feral dogs (Eisenberg, 1989). Considered "Near Threatened" by IUCN, the species is also listed in CITES Appendix II. It originally ranged from the Cordillera Central de Colombia to southern (Huacabamba region) and northern Ecuador, and northern and central Peru (Figure 3).

There are huge gaps in our knowledge on the basic biology and ecology of this species; even its presence or absence in some parts of the Northern Andes has never been reliably documented. No information on the reproductive biology or any other aspect of the biology of the species is available other than the original taxonomic work by Hershkovitz (1982) in Eisenberg (1989).

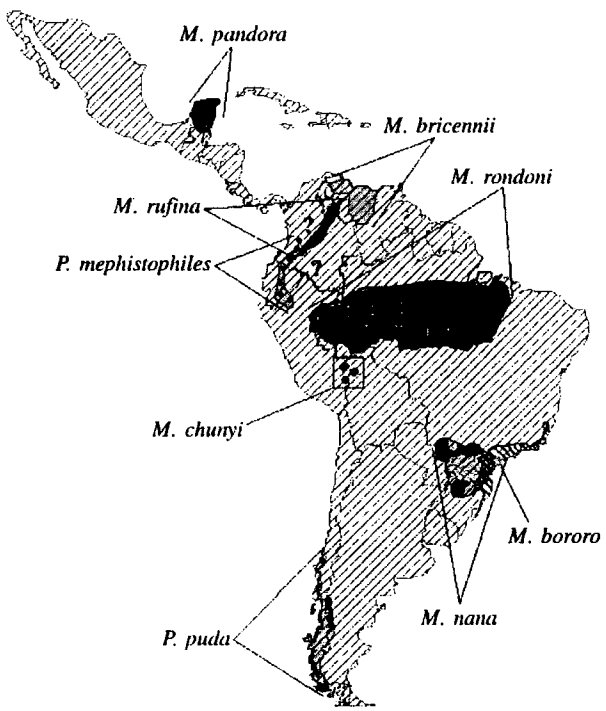

FIGURE 3. Historic distribution (grey) and predicted current distribution (black) of all the species of the genus *Mazama* with none overlapping in their distributions and the two species of pudu (*Pudu puda* and *P. mephistophiles*) in Latin America. For *M. rondoni* a combination of historic and current/predicted distribution (chess board pattern) is provided given the lack of biological information. The three historical records of *M. chunyi* available in the literature are ploted as distribution. The original distribution of the Brazilian Atlantic Forest (inverse diagonal lines) could be the historic distribution of *M. bororo*.

SOUTHERN PUDU (PUDU PUDA)

Weighing less than 12 kg, the southern pudu is considered the smallest deer in the world (Eldridge, MacNamara & Pacheco,1987). It is considered vulnerable by IUCN and is listed in CITES Appendix I. Although, it has been intensively studied in captivity, especially its endocrinology (Bubenik *et al.*, 2000), it remains poorly known in the wild. As is the case for the northern pudu, predation by dogs, competition with introduced species (such as red and Sika deer), and hunting are considered significant threats (Figure 3).

The southern pudu occurs in a wide variety of habitat types throughout its range in Chile and Argentina, but is characteristically found in thick forests dominated by *Nothofagus* spp., from sea level to 1,000 m. Bamboo thickets and paramo grassland are also favoured (Eisenberg, 1989). Other than this, little is known about the ecology of this South American species (Dellafiore & Maceira, 2001).

THE SOUTH AMERICAN BROCKET DEER SPECIES COMPLEX: A CONUNDRUM?

There has been considerable recent interest in the taxonomy and systematics of the genus *Mazama* since the discovery (or re-discovery) of two or three new species (Duarte & Jorge, 1996; Duarte & Merino, 1997; Medellin, Gardner & Aranda, 1998). The large variation in morphology at both the species and subspecies level in *M. americana* and *M. gouazoubira* has attracted considerable attention from geneticists and taxonomists in Latin America and elsewhere (Jorge & Benirschke, 1977; Smith *et al.*, 1986; Neitzel, 1987; Duarte, 1998).

RED BROCKET DEER (MAZAMA AMERICANA)

The red brocket deer is the most widely distributed deer in Latin America (Figure 4), with 16 subspecies described to date, though many taxonomic riddles remain unresolved. It is highly variable in colour, size, and morphology across its range. It may be a habitat specialist in parts of its distribution, where a preference for pristine tropical rain forest is apparent (Leopold, 1959; Eisenberg, 1989; M. Weber, unpubl. data). The species has only recently been studied in the wild and in captivity in Suriname, Brazil, and Mexico (Branan, Werkhoven & Marchinton, 1985; Branan & Marchinton, 1987; Duarte, 1992; Weber, 2000). The red brocket has been recorded as far north as El Cielo Biosphere Reserve, Tamaulipas, in the north of Mexico and in the Yucatan Peninsula in the south (Weber & Reyna-Hurtado, 1999). An ongoing long-term project addressing aspects of red brocket deer biology and ecology in the wild is being carried out in the Calakmul Biosphere Reserve, Campeche, Mexico (Weber & Reyna-Hurtado, 1999; Weber, 2000). In spite of its relatively wide distribution throughout tropical environments in Mexico, the red brocket deer has been little studied and large gaps in knowledge of its biology and

FIGURE 4. Predicted current distribution of *Mazama americana* (black blurred) and *Mazama gouazoubira* (grey solid) in Latin America. Note the large range overlap in north-central South America and compare with Figure 3 for overlapping with other species of the genus *Mazama*.

ecology remain unresolved in this country. No reliable information exists to assess its conservation status or even range changes, so we report only historical distribution.

There is no information on this species' conservation status for most Central American countries. Some baseline research on the conservation status and abundance has been carried out in Guatemala (MacNab, 1998) and Panama (Wright *et al.*, 2000). Poaching and subsistence hunting is pervasive in Central America, and local extinctions of the deer fauna may be occurring in many areas (Wright *et al.*, 2000) (Figure 4).

There is considerable variation in the body size of the red brocket deer (*e.g.*, > 60 kg in Argentina and 10 to 15 kg in northern Guatemala), colour (from a deep reddish in the northern subspecies to a more pale, almost yellowish colour in some South American races) and other traits (Eisenberg, 1989; Duarte, 1998).

Due largely to its solitary nature, its secretive habits, and the relatively inaccessible places it inhabits, the red brocket has been little studied in South America (Leopold, 1959; Wemmer, 1998). Most studies have simply relied on the information obtained from native hunters to document aspects of its biology such as diet (Branan, Werkhoven & Marchinton, 1985; Bisbal, 1994), herbivory (Bodmer, 1989), and reproductive biology (Branan & Marchinton, 1987).

Grey brocket deer (Mazama gouazoubira)

There are nine subspecies of grey brocket deer described, but the taxonomy of the group is unclear (Hershkovitz, 1959; Eisenberg, 1989), and there could be more species masked by the grey brocket complex. It is a habitat generalist, highly resistant to hunting and habitat modification (Redford & Eisenberg, 1989; Dellafiore & Maceira, 2001), but subject to high hunting pressure throughout its range (Yanosky & Mercoli, 1994). It has been studied in Argentina (Yanosky & Mercoli, 1994), Brazil (Pinder & Leeuwenberg, 1997; Duarte, 1998), the Bolivian and Paraguayan Chaco region, and Peru (Bodmer, 1991; J. L. Cartes, pers. comm.), but no information on its conservation status is available. An endemic subspecies of grey brocket deer (*M. g. permira*) is present on San Jose Island, Panama (Eisenberg, 1989) (Figure 4).

Yucatan Peninsula brown brocket deer (Mazama pandora)

The recently rediscovered Yucatan Peninsula brown brocket (Medellin, Gardner & Aranda, 1998) is endemic to the Yucatan Peninsula (Mexico, Belize, and Northern Guatemala), where it occurs as a habitat generalist and highly adaptable deer. Its biology and ecology have been under study since 1996 in southeastern Mexico (Weber & Reyna-Hurtado, 1999; Weber, 2000). Although its historical distribution range is unknown, some data suggest that it may be stable in most of the habitat in which it is actually found (M. Weber, unpubl. data) (Figure 3).

In Guatemala, the Yucatan Peninsula brown brocket is probably present in small numbers (compared with the more abundant red brocket) in Tikal National Park and some other areas of the Maya Biosphere Reserve (R. B. MacNab, pers. comm.). No information is available for Belize, but the species is likely to be present in the Gallon Jug-Rio Bravo conservation and management area in the region bordering Mexico and Guatemala (M. Weber, pers. observ.) (Figure 3).

Small grey brocket deer (Mazama rondoni)

The small grey brocket deer was described at the beginning of the last century and just recently confirmed by cytogenetics (de Miranda Ribeiro, 1919; Duarte, 1998). This deer is the subrogate form of *M. gouazoubira* in the Amazonian rainforest. The biology of this species is completely unknown, but it may be threatened by overhunting and habitat destruction in parts of its range, which is within the Amazon rainforest in Brazil, Peru, and perhaps also in Bolivia (Duarte, 1998) (Figure 3).

Brazilian dwarf brocket deer (Mazama nana)

The biology and ecology of the Brazilian dwarf brocket deer are poorly documented, but its distribution is known to overlap that of the red and grey brocket deer and part of that of *M. bororo*. Wild populations are currently being studied in Argentina (Dellafiore & Maceira, 2001) and in controlled captive conditions in Brazil (Duarte, 1998). We estimate a 40% reduction in historic distribution based on current habitat destruction patterns in its normal habitat (Figure 3).

Colombian dwarf brocket deer (Mazama rufina)

The taxonomy of the Colombian dwarf brocket deer is unresolved. Some authors consider it to be the same species as the Peruvian and Brazilian dwarf brockets or

even to be a subspecies of the more common and widespread red brocket deer (Eisenberg, 1989). Its biology and ecology are totally unknown, partly because it is distributed in an area with high social unrest that makes research difficult. There are no studies or research projects on this species to date (Figure 3).

PERUVIAN DWARF BROCKET DEER (MAZAMA CHUNYI)

The Peruvian dwarf brocket deer is the smallest brocket deer, with a body weight of less than 14 kg. This species was described by Hershkovitz (1959). Its biology is completely unknown as it is rarely seen. It was reported for the first time for the Yungas Province in Bolivia in 1996 (Yensen, Tarifa & Anderson, 1994; Ergueta & Morales, 1996), prior to which just a handful of museum records existed, so its geographic distribution remains unclear (Figure 3). One research project working on the region where the first record in Bolivia was obtained is trying to document baseline biology and ecology of the species (M. Pardo, pers. comm.).

GREY DWARF BROCKET DEER (MAZAMA BRICENNII)

The grey dwarf brocket deer is another brocket deer with unresolved taxonomy: some people claim that it is a distinct species, while others consider it to be continuous with the other three dwarf brockets (Eisenberg, 1989; Duarte, 1998). The biology of this species is totally unknown, but it probably is highly endangered by habitat destruction since it inhabits the mist forests of the Andean Venezuelan Cordillera (Eisenberg, 1987; 1989). There are no studies to date. For this species we developed a predicted distribution map based on potential habitat and historic records, but given the lack of information this map should be viewed with caution (Figure 3).

BRAZILIAN ATLANTIC FOREST DEER (MAZAMA BORORO)

In 1996 it was proposed based on cytogenetics that the Brazilian Atlantic forest deer is distinct from the red brocket deer (Duarte & Jorge, 1996; Duarte, 1996; 1998). Considered endemic to the Atlantic forest of Brazil, one of the most endangered forest ecosystems on earth, this species is likely to be highly endangered. If it is found only in the Atlantic forest, then it is one of the most endangered deer in the world, with its habitat reduced to less than 2% of its original size (Figure 3).

DIVERSITY PATTERNS AND RESEARCH TRENDS BY REGION

MEXICO

To date, almost all research in Mexico has focused on the white-tailed deer, with little effort made to study the two brocket species and the mule deer (Galindo-Leal, 1994; Weber & Galindo-Leal, 1994; Galindo-Leal & Weber, 1998). Most research has been in oak-pine forests and semi-arid environments, though there has been some deer work done in tropical environments (Mandujano & Gallina, 1995).

The highest deer diversity in Mexico is found in the southern tropical semi-deciduous forests of the Yucatan Peninsula (Peten region), where three sympatric species (*O. virginianus*, *Mazama americana*, and *M. pandora*) exist.

CENTRAL AMERICA

Almost all research in Central America has been carried out in protected areas and national parks in Costa Rica and Panama; the status of deer in Belize, El Salvador, Guatemala, Honduras, and Nicaragua remains almost unknown (Mendez, 1984). Subsistence hunting in countries like El Salvador and Panama might be responsible for extensive local extinctions of species in many areas (Wright *et al.*, 2000; F. Horgan, pers. comm.). Baseline research on distribution, abundance, and conservation management of species is urgently required in these countries. The highest deer diversity in the region is found in northern Guatemala (Peten region), with the same deer assemblage as in the Yucatan, Mexico.

SOUTH AMERICA

Most deer research in South America has concentrated on highly endangered species such as the pampas, huemul and marsh deer (Wemmer, 1998; Duarte, 1992; 1996; Duarte & Jorge, 1996; Duarte & Merino, 1997; Gonzalez *et al.*, 1998). Research has focused on taxonomy, genetics, population ecology, behaviour, survey methodology, and, in recent years, disease aspects concerning conservation medicine (Povilitis, 1983; 1984; Jackson, 1985; 1986; Spotorno, Brum & Tomaso, 1987; Duarte, 1992; Beccaceci, 1996; Pinder, 1996; Mathias, Girio & Duarte, 1999; Mourao *et al.*, 2000; Dellafiore & Maceira, 2001; Duarte *et al.*, 2001; Frid, 2001).

The brocket deer species were largely ignored until very recently, when the discovery of the Yucatan brown brocket and Brazilian Atlantic forest brocket attracted renewed attention to both the red and grey brocket deer complexes (Duarte, 1996; Medellin, Gardner & Aranda, 1998).

The largest diversity of tropical deer in the continent is found in the southern Brazil, northern Argentina, and eastern Paraguay region known as the Parana River Basin and Delta, where potentially as many as five species coexist or may have co-existed in the past (but see overlap areas in Figures 1, 2, and 3). Another region with high deer diversity is found in Peru and Bolivia's Andean Yungas region, where originally there may have been as many as four or five sympatric species.

Discussion

DEER CONSERVATION CHALLENGES IN LATIN AMERICA

Intensive exploitation of South American cervids followed European settlement of the continent and was probably localized initially on the accessible Pampas grasslands and rangelands of Chile and Argentina. pampas deer, for example, were hunted intensively during the 19th century and their hides were processed on a vast scale: over two million were exported between 1860 and 1870 (Thornback & Jenkins, 1982). Subsistence hunting is a major threat to all deer in the region (Galindo-Leal & Weber, 1998; Peres, 2000), whereas habitat destruction and fragmentation are important threats to tropical and Andean deer (Frid, 2001).

Recent studies in Latin America have demonstrated that subsistence hunting is still a major activity for rural

human populations (Robinson & Bennett, 1999; Escamilla *et al.*, 2000; Peres, 2000). Together with peccaries (*Tayassu* spp.) and some large caviomorph rodents (*e.g.*, *Agouti* spp.), deer are the most preferred targets of these hunters (Peres, 2000). In fact, deer are one of the most important sources of animal protein in rural Latin America (Weber, 2000). For example, data gathered during a three-month period in southeastern Mexico from a population of 155 peasant families in eight communities that regularly practiced subsistence hunting demonstrated that deer harvest accounted for 48% of the total biomass (10,095 kg) in a harvest bag comprising 13 wildlife species (Weber, 2000).

Considerable effort has been expended on studies of population ecology, behaviour, and captive breeding of some species, but there has been little management-oriented research (Weber & Galindo-Leal, 1994). We consider that manipulative (adaptive management) experiments (*e.g.*, changing hunting quotas and bags while researching their effects on population dynamics) with white-tailed, mule, and brocket deer would be useful for adapting management strategies while learning in the process (*e.g.*, on over-abundant white-tailed deer herds in northeast Mexico) (Galindo-Leal & Weber, 1998).

Biodiversity is currently being lost around the world at an alarming rate, and many deer in Latin America are among the species at risk. The most threatened genera are *Blastocerus*, *Hippocamelus*, *Ozotoceros*, *Pudu*, and *Mazama* (Wemmer, 1998). A number of deer are also prime examples of flagship and umbrella species, whose continued survival is related to the complex interplay of flora and fauna. Many species of deer are now under great threat of extinction, and the situation will not change for the better without a concerted effort.

Almost half of the Latin American native deer taxa are threatened to some degree (Table I). Hunting, deforestation, overgrazing, diseases, feral dogs, and competition with introduced deer and livestock are the main reasons of concern (Wemmer, 1998).

Although deer research in Latin America has accelerated considerably since the early 1980s, large gaps in knowledge on the biology of particular species still exist. Increased collaboration with deer scientists from developed countries for the study of native deer species should be encouraged. Priorities for species conservation programs include the pampas, marsh, and Andean (huemul, taruca, and pudus) deer, while priorities for species research programs include the Andean deer (mainly taruca and pudus) and both the red brocket and grey brocket deer complexes. Regional priorities for further research and conservation include (not in order of priority) Meso-America from the Yucatan Peninsula to Panama, the Andes, the Yungas region in Peru and Bolivia, the Parana-Paraguay river basins, and the Amazon River basin.

All Latin American countries with native deer populations should be supported in efforts to preserve large natural areas harbouring intact communities of wildlife. The promotion of conservation is a great challenge when countries also have to address critical socio-economic situations. Conservation initiatives for large flagship species, such as endemic deer, will require incentives, encouragement, and financing.

RECOMMENDATIONS FOR FUTURE WORK

In order to develop ecologically sound conservation strategies for Latin American deer, we need to obtain reliable baseline biological information for poorly known species as soon as possible. Research needs to be focused on population estimation methodologies, habitat conservation, and sustainable use.

We need to encourage graduate students in conservation biology to get back to the study of deer natural history before we can even think of having deer managers. Multinational collaboration in the study of species with large distribution ranges should be a priority. The "Mazama riddle", as it is commonly called, deserves renewed attention, as the discovery of new species is likely.

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Appendix II.

List of all observations of deer used in this study. The observations with geographical coordinates correspond to those used in the spatial analysis of Chapter four. The rest are observations in transects (either permanent or temporary), material collected from hunting (skulls or stomach samples or both) during the course of this study and deer skulls previously collected by other researchers and deposited at the Zoology Museum of ECOSUR (El Colegio de la Frontera Sur = EZM), Quintana Roo, Mexico.

Species	Type of observation	Place of observation	Area	Lat. Grad.	Lat. Min.	Lat. Sec.	Long. Grad.	Lon. Min.	Long. Sec.	Source
Mazama americana	Hunting	TEF	Nuevo Becal	18	42	58.38	89	19	46.99	This study
Mazama americana	Hunting	TEF	GCR	18	34	3.91	89	16	58.8	This study
Mazama americana	Hunting	TEF	Nuevo Becal	18	43	13.56	89	13	22.08	This study
Mazama americana	Hunting	LFF	Nuevo Becal	18	43	29.21	89	18	0.93	This study
Mazama americana	Hunting	TEF	Nuevo Becal	18	44	30	89	18	10	This study
Mazama americana	Hunting	TEF	Nuevo Becal	18	47	30.19	89	11	41.68	This study
Mazama americana	Hunting	TEF	Nuevo Becal							This study
Mazama americana	Sighting	Temporary transects	Nuevo Becal	18	44	10	89	18	0	This study
Mazama americana	Sighting	Permanent transects	Nuevo Becal	18	39	58.06	89	12	43.72	This study
Mazama americana	Sighting	TEF	Nuevo Becal	18	45	4	89	14	46	This study
Mazama americana	Hunting	TEF	Nuevo Becal							This study
Mazama americana	Hunting	TEF	Nuevo Becal							This study
Mazama americana	Hunting	TEF	Nuevo Becal							This study
Mazama americana	Hunting	TEF	Nuevo Becal							This study
Mazama americana	Hunting	TEF	Nuevo Becal							This study
Mazama americana	Hunting	A	Nuevo Becal							This study
Mazama americana	Hunting	TEF	Nuevo Becal							This study
Mazama americana	Hunting	TEF	GCR	18	6	27.42	89	49	8.5	This study
Mazama americana	Hunting	TEF	Nuevo Becal							This study
Mazama americana	Hunting	TEF	Nuevo Becal	18	44	30	89	18	10	This study
Mazama americana	Sighting	Temporary transects	Nuevo Becal							This study
Mazama americana	Sighting	Temporary transects	Nuevo Becal							This study
Mazama americana	Sighting	Temporary transects	Nuevo Becal							This study

Species	Type of observation	Place of observation	Area	Lat. Grad.	Lat. Min.	Lat. Sec.	Long. Grad.	Lon. Min.	Long. Sec.	Source
Mazama americana	Sighting	Unrecorded	Nuevo Becal							EZM
Mazama americana	Sighting	Unrecorded	Nuevo Becal							EZM
Mazama americana	Sighting	Temporary transects	Nuevo Becal							This study
Mazama americana	Sighting	Temporary transects	Nuevo Becal							This study
Mazama americana	Sighting	Unrecorded	Nuevo Becal							EZM
Mazama americana	Sighting	Unrecorded	Nuevo Becal							EZM
Mazama americana	Sighting	Permanent transects	Nuevo Becal	18	42	58.38	89	19	46.99	This study
Mazama americana	Hunting	SG	Nuevo Becal							This study
Mazama americana	Hunting	TEF	Nuevo Becal							This study
Mazama americana	Hunting	TEF	Nuevo Becal	18	39	58.06	89	12	43.72	This study
Mazama americana	Hunting	TEF	Nuevo Becal							This study
Mazama americana	Hunting	TEF	Nuevo Becal	18	44	46.52	89	14	29.75	This study
Mazama americana	Hunting	TEF	Nuevo Becal	18	37	44.75	89	11	14.72	This study
Mazama americana	Hunting	TEF	Nuevo Becal	18	45	6.48	89	17	5.89	This study
Mazama americana	Sighting	Temporary transects	Nuevo Becal	18	40	34.09	89	12	36.82	This study
Mazama americana	Sighting	Temporary transects	Nuevo Becal	18	47	30.19	89	11	41.68	This study
Mazama americana	Sighting	TEF	Nuevo Becal	18	39	58.06	89	12	43.72	This study
Mazama americana	Sighting	Temporary transects	Nuevo Becal	18	45	7.71	89	18	8.54	This study
Mazama americana	Sighting	Permanent transects	Nuevo Becal	18	39	58.06	89	12	43.72	This study
Mazama americana	Hunting	TEF	Nuevo Becal	18	36	10.03	89	15	40.04	This study
Mazama americana	Sighting	Permanent transects	Nuevo Becal	18	35	52.59	89	14	45.87	This study
Mazama americana	Sighting	TEF	Nuevo Becal	18	39	58.06	89	12	43.72	This study
Mazama americana	Hunting	TEF	Nuevo Becal							This study
Mazama americana	Hunting	Unrecorded	GCR	17	52	30	89	30	0	This study
Mazama americana	Hunting	Unrecorded	GCR	17	52	30	89	30	0	This study
Mazama americana	Hunting	Unrecorded	GCR	18	45	6.48	89	17	5.89	This study
Mazama americana	Hunting	Unrecorded	GCR	18	43	13.56	89	13	22.08	This study
Mazama americana	Hunting	Unrecorded	GCR							This study
Mazama americana	Hunting	Unrecorded	GCR							This study
Mazama americana	Hunting	Unrecorded	GCR	18	36	33.03	89	19	41.25	This study
Mazama americana	Hunting	Unrecorded	GCR	18	26	39	89	18	0	This study

Species	Type of observation	Place of observation	Area	Lat. Grad.	Lat. Min.	Lat. Sec.	Long. Grad.	Lon. Min.	Long. Sec.	Source
Mazama americana	Sighting	Permanent transects	GCR							This study
Mazama americana	Sighting	SG	GCR							EZM
Mazama americana	Sighting	LFF	GCR							EZM
Mazama americana	Sighting	TEF	GCR							EZM
Mazama americana	Sighting	Unrecorded	GCR							EZM
Mazama americana	Sighting	TEF	GCR							EZM
Mazama americana	Sighting	LFF	GCR							EZM
Mazama americana	Sighting	TEF	GCR							EZM
Mazama americana	Sighting	Permanent transects	Nuevo Becal	18	35	30	89	25	0	This study
Mazama americana	Sighting	Permanent transects	Nuevo Becal	18	47	30.19	89	11	41.68	This study
Mazama americana	Sighting	Permanent transects	Nuevo Becal							This study
Mazama americana	Sighting	TEF	Nuevo Becal	18	35	30	89	25	0	This study
Mazama pandora	Hunting	TEF	Nuevo Becal	18	36	10.03	89	15	40.04	This study
Mazama pandora	Hunting	TEF	GCR							This study
Mazama pandora	Hunting	SG	Nuevo Becal	18	44	50.21	89	17	56.43	This study
Mazama pandora	Hunting	Unrecorded	Nuevo Becal	18	44	50.21	89	17	56.43	This study
Mazama pandora	Hunting	TEF	Nuevo Becal	18	45	6	89	17	6	This study
Mazama pandora	Hunting	TEF	Nuevo Becal							This study
Mazama pandora	Hunting	LFF	Nuevo Becal							This study
Mazama pandora	Hunting	TEF	Nuevo Becal							This study
Mazama pandora	Hunting	Unrecorded	Nuevo Becal							This study
Mazama pandora	Hunting	TEF	Nuevo Becal	18	44	10	89	18	0	This study
Mazama pandora	Hunting	Unrecorded	Nuevo Becal							This study
Mazama pandora	Hunting	A	Nuevo Becal							This study
Mazama pandora	Hunting	TEF	Nuevo Becal							This study
Mazama pandora	Hunting	TEF	Nuevo Becal							This study
Mazama pandora	Hunting	Unrecorded	Nuevo Becal							This study
Mazama pandora	Hunting	Unrecorded	Nuevo Becal							This study
Mazama pandora	Hunting	LFF	Nuevo Becal	18	43	10	89	22	30	This study
Mazama pandora	Hunting	Unrecorded	Nuevo Becal							This study
Mazama pandora	Hunting	A	Nuevo Becal							This study
Mazama pandora	Hunting	LFF	Nuevo Becal							This study
Mazama pandora	Sighting	LFF	Nuevo Becal	18	13	0	89	22	30	This study

Species	Type of observation	Place of observation	Area	Lat. Grad.	Lat. Min.	Lat. Sec.	Long. Grad.	Lon. Min.	Long. Sec.	Source
Mazama pandora	Sighting	TEF	Nuevo Becal	18	43	10	89	22	30	This study
Mazama pandora	Sighting	LFF	Nuevo Becal	18	44	30	89	18	10	This study
Mazama pandora	Sighting	Permanent transects	Nuevo Becal							This study
Mazama pandora	Hunting	LFF	Nuevo Becal							This study
Mazama pandora	Hunting	TEF	Nuevo Becal	18	44	30	89	18	10	This study
Mazama pandora	Hunting	LFF	Nuevo Becal	18	21	20	89	32	0	This study
Mazama pandora	Hunting	Unrecorded	GCR							This study
Mazama pandora	Hunting	LFF	Nuevo Becal	19	45	39	89	50	55	This study
Mazama pandora	Hunting	TEF	Nuevo Becal	18	44	30	89	18	10	This study
Mazama pandora	Hunting	TEF	Nuevo Becal	18	43	13.56	89	13	22.08	This study
Mazama pandora	Hunting	LFF	Nuevo Becal	18	48	47.03	89	19	34.34	This study
Mazama pandora	Hunting	TEF	Nuevo Becal							This study
Mazama pandora	Sighting	Permanent transects	Nuevo Becal	18	43	29.21	89	18	0.93	This study
Mazama pandora	Sighting	Permanent transects	Nuevo Becal	18	42	58.38	89	19	46.99	This study
Mazama pandora	Sighting	LFF	Nuevo Becal	18	42	58.38	89	19	46.99	This study
Mazama pandora	Hunting	LFF	Nuevo Becal	18	42	58.38	89	19	46.99	This study
Mazama pandora	Hunting	Unrecorded	Nuevo Becal	18	42	58.38	89	19	46.99	This study
Mazama pandora	Hunting	LFF	Nuevo Becal	18	8	10	89	45	28	This study
Mazama pandora	Sighting	SG	GCR							EZM
Mazama pandora	Sighting	Permanent transects	GCR							This study
Mazama pandora	Sighting	Unrecorded	GCR							EZM
Mazama pandora	Sighting	LFF	GCR							EZM
Mazama pandora	Sighting	TEF	GCR							EZM
Mazama pandora	Sighting	SG	GCR							EZM
Mazama pandora	Sighting	Temporary transects	Nuevo Becal	18	36	33.03	89	19	41.25	This study
Mazama pandora	Sighting	Permanent transects	Nuevo Becal	18	36	30.53	89	16	23.17	This study
Mazama pandora	Sighting	TEF	Nuevo Becal	18	34	3.91	89	16	58.8	This study
Mazama pandora	Sighting	Permanent transects	Nuevo Becal	18	40	0.82	89	15	5.75	This study
Mazama pandora	Sighting	Temporary transects	Nuevo Becal	18	43	13.56	89	13	22.08	This study
Mazama pandora	Hunting	SG	Nuevo Becal	18	41	21.75	89	12	57.35	This study
Mazama pandora	Hunting	Unrecorded	GCR	18	34	3.91	89	16	58.8	This study
Mazama pandora	Hunting	Unrecorded	Nuevo Becal							This study
Mazama pandora	Hunting	LFF	Nuevo Becal	18	41	42.15	89	10	51.69	This study

Species	Type of observation	Place of observation	Area	Lat. Grad.	Lat. Min.	Lat. Sec.	Long. Grad.	Lon. Min.	Long. Sec.	Source
Mazama pandora	Hunting	SG	Nuevo Becal	18	47	30.19	89	11	41.68	This study
Mazama pandora	Hunting	Unrecorded	GCR	18	35	30	89	25	0	This study
Mazama pandora	Hunting	Unrecorded	Nuevo Becal							This study
Mazama pandora	Hunting	Unrecorded	Nuevo Becal	18	36	33.03	89	19	41.25	This study
Mazama pandora	Hunting	TEF	Nuevo Becal							This study
Mazama pandora	Hunting	Unrecorded	Nuevo Becal							This study
Mazama pandora	Hunting	LFF	Nuevo Becal							This study
Mazama pandora	Hunting	Unrecorded	Nuevo Becal	18	26	39	89	18	0	This study
Mazama pandora	Sighting	TEF	Nuevo Becal							EZM
Mazama pandora	Sighting	Temporary transects	Nuevo Becal							This study
Mazama pandora	Hunting	LFF	Nuevo Becal							This study
Mazama pandora	Hunting	Unrecorded	Nuevo Becal							This study
Mazama pandora	Hunting	Unrecorded	Nuevo Becal							This study
Mazama pandora	Hunting	Unrecorded	Nuevo Becal							This study
Mazama pandora	Hunting	Unrecorded	Nuevo Becal	18	26	39	89	18	0	This study
Mazama pandora	Sighting	Temporary transects	Nuevo Becal							This study
Mazama pandora	Sighting	Permanent transects	Nuevo Becal	18	38	12.93	89	15	18.73	This study
Mazama pandora	Hunting	LFF	Nuevo Becal	18	38	12.93	89	15	18.73	This study
Mazama pandora	Hunting	Unrecorded	Nuevo Becal	18	39	58.06	89	12	43.72	This study
Mazama pandora	Sighting	Temporary transects	Nuevo Becal	18	47	30.19	89	11	41.68	This study
Mazama pandora	Sighting	Permanent transects	Nuevo Becal	18	47	30.19	89	11	41.68	This study
Mazama pandora	Sighting	Permanent transects	Nuevo Becal	18	39	58.06	89	12	43.72	This study
Mazama pandora	Sighting	TEF	Nuevo Becal	18	34	3.91	89	16	58.8	This study
Mazama pandora	Sighting	TEF	Nuevo Becal	18	40	0.82	89	15	5.75	This study
Mazama pandora	Sighting	Temporary transects	Nuevo Becal	18	44	10	89	18	0	This study
Mazama pandora	Sighting	Permanent transects	Nuevo Becal	18	34	3.91	89	16	58.8	This study
Mazama pandora	Sighting	TEF	Nuevo Becal	18	34	3.91	89	16	58.8	This study
Mazama pandora	Sighting	TEF	Nuevo Becal	18	38	12.93	89	15	18.73	This study
Mazama pandora	Sighting	TEF	Nuevo Becal	18	39	58.06	89	12	43.72	This study
Mazama pandora	Sighting	TEF	GCR	18	8	10	89	45	28	This study
Mazama pandora	Sighting	LFF	GCR	18	8	10	89	45	28	This study
Mazama pandora	Sighting	SG	GCR	18	8	10	89	45	28	This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal							This study

Species	Type of observation	Place of observation	Area	Lat. Grad.	Lat. Min.	Lat. Sec.	Long. Grad.	Lon. Min.	Long. Sec.	Source
Odocoileus virginianus	Hunting	TEF	Nuevo Becal	18	40	34.09	89	12	36.82	This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal							This study
Odocoileus virginianus	Hunting	TEF	GCR	18	34	3.91	89	16	58.8	This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal							This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal							This study
Odocoileus virginianus	Hunting	Unrecorded	GCR	18	34	3.91	89	16	58.8	This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal	18	41	21.75	89	12	57.35	This study
Odocoileus virginianus	Hunting	A	Nuevo Becal	18	37	30	89	17	30	This study
Odocoileus virginianus	Hunting	Unrecorded	GCR	18	35	26.94	89	15	30.08	This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal							This study
Odocoileus virginianus	Hunting	SG	Nuevo Becal							This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal							This study
Odocoileus virginianus	Hunting	SG	Nuevo Becal							This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal	18	36	25.7	89	16	49.19	This study
Odocoileus virginianus	Hunting	TEF	Nuevo Becal	18	44	50.21	89	17	56.43	This study
Odocoileus virginianus	Hunting	A	Nuevo Becal	18	44	50.21	89	17	56.43	This study
Odocoileus virginianus	Hunting	TEF	Nuevo Becal							This study
Odocoileus virginianus	Sighting	LFF	GCR	18	44	50.21	89	17	56.43	This study
Odocoileus virginianus	Sighting	TEF	GCR	18	8	10	89	45	28	This study
Odocoileus virginianus	Hunting	Unrecorded	GCR							This study
Odocoileus virginianus	Hunting	Unrecorded	GCR							This study
Odocoileus virginianus	Hunting	Unrecorded	GCR	18	6	27.42	89	49	8.5	This study
Odocoileus virginianus	Hunting	Unrecorded	GCR	18	6	27.42	89	49	8.5	This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal	18	19	40	89	50	25	This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal	18	48	47.03	89	19	34.34	This study
Odocoileus virginianus	Sighting	Temporary transects	Nuevo Becal	18	48	47.03	89	19	34.34	This study
Odocoileus virginianus	Sighting	Unrecorded	Nuevo Becal							This study
Odocoileus virginianus	Sighting	TEF	Nuevo Becal							This study
Odocoileus virginianus	Hunting	LFF	Nuevo Becal							This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal							This study
Odocoileus virginianus	Hunting	A	Nuevo Becal							This study
Odocoileus virginianus	Sighting	Temporary transects	Nuevo Becal							This study
Odocoileus virginianus	Sighting	Temporary transects	Nuevo Becal							This study

Species	Type of observation	Place of observation	Area	Lat. Grad.	Lat. Min.	Lat. Sec.	Long. Grad.	Lon. Min.	Long. Sec.	Source
Odocoileus virginianus	Sighting	Temporary transects	Nuevo Becal							This study
Odocoileus virginianus	Sighting	Permanent transects	Nuevo Becal							This study
Odocoileus virginianus	Hunting	TEF	Nuevo Becal							This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal							This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal							This study
Odocoileus virginianus	Hunting	SG	Nuevo Becal	18	48	47.03	89	19	34.34	This study
Odocoileus virginianus	Sighting	Permanent transects	Nuevo Becal							This study
Odocoileus virginianus	Sighting	A	Nuevo Becal							This study
Odocoileus virginianus	Sighting	Temporary transects	Nuevo Becal	18	48	47.03	89	19	34.34	This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal							This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal							This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal							This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal							This study
Odocoileus virginianus	Sighting	Temporary transects	Nuevo Becal							This study
Odocoileus virginianus	Sighting	Temporary transects	Nuevo Becal							This study
Odocoileus virginianus	Hunting	SG	Nuevo Becal							This study
Odocoileus virginianus	Hunting	TEF	Nuevo Becal							This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal							This study
Odocoileus virginianus	Hunting	TEF	Nuevo Becal							This study
Odocoileus virginianus	Sighting	Temporary transects	Nuevo Becal							This study
Odocoileus virginianus	Sighting	TEF	Nuevo Becal							EZM
Odocoileus virginianus	Hunting	A	Nuevo Becal							This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal							This study
Odocoileus virginianus	Hunting	TEF	Nuevo Becal							This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal	18	43	29.21	89	18	0.93	This study
Odocoileus virginianus	Sighting	Permanent transects	Nuevo Becal							This study
Odocoileus virginianus	Sighting	TEF	Nuevo Becal							EZM
Odocoileus virginianus	Sighting	Permanent transects	Nuevo Becal							This study
Odocoileus virginianus	Sighting	TEF	Nuevo Becal							EZM
Odocoileus virginianus	Sighting	TEF	Nuevo Becal							EZM
Odocoileus virginianus	Sighting	Temporary transects	Nuevo Becal							This study
Odocoileus virginianus	Sighting	TEF	Nuevo Becal							EZM
Odocoileus virginianus	Sighting	Permanent transects	Nuevo Becal							This study

Species	Type of observation	Place of observation	Area	Lat. Grad.	Lat. Min.	Lat. Sec.	Long. Grad.	Lon. Min.	Long. Sec.	Source
Odocoileus virginianus	Sighting	Temporary transects	Nuevo Becal							This study
Odocoileus virginianus	Sighting	TEF	Nuevo Becal							EZM
Odocoileus virginianus	Sighting	TEF	Nuevo Becal							EZM
Odocoileus virginianus	Sighting	Unrecorded	Nuevo Becal							EZM
Odocoileus virginianus	Sighting	Permanent transects	Nuevo Becal	18	43	29.21	89	18	0.93	This study
Odocoileus virginianus	Sighting	Permanent transects	Nuevo Becal	18	42	58.38	89	19	46.99	This study
Odocoileus virginianus	Sighting	Unrecorded	Nuevo Becal							EZM
Odocoileus virginianus	Sighting	A	Nuevo Becal							EZM
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal							This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal							This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal							This study
Odocoileus virginianus	Sighting	A	Nuevo Becal							EZM
Odocoileus virginianus	Sighting	TEF	Nuevo Becal							EZM
Odocoileus virginianus	Sighting	TEF	Nuevo Becal							EZM
Odocoileus virginianus	Sighting	Permanent transects	Nuevo Becal							This study
Odocoileus virginianus	Sighting	TEF	Nuevo Becal							This study
Odocoileus virginianus	Sighting	TEF	Nuevo Becal							This study
Odocoileus virginianus	Sighting	Unrecorded	Nuevo Becal							EZM
Odocoileus virginianus	Sighting	Unrecorded	Nuevo Becal							EZM
Odocoileus virginianus	Sighting	Unrecorded	Nuevo Becal							EZM
Odocoileus virginianus	Sighting	Temporary transects	Nuevo Becal							This study
Odocoileus virginianus	Sighting	TEF	Nuevo Becal							This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal							This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal	18	42	58.38	89	19	46.99	This study
Odocoileus virginianus	Hunting	Unrecorded	Nuevo Becal	18	42	58.38	89	19	46.99	This study
Odocoileus virginianus	Hunting	Unrecorded	GCR	18	8	10	89	45	28	This study
Odocoileus virginianus	Sighting	Unrecorded	GCR							EZM
Odocoileus virginianus	Sighting	TEF	GCR							This study
Odocoileus virginianus	Sighting	SG	GCR							This study
Odocoileus virginianus	Sighting	SG	GCR							This study
Odocoileus virginianus	Sighting	TEF	GCR							This study
Odocoileus virginianus	Hunting	Unrecorded	GCR							This study
Odocoileus virginianus	Hunting	Unrecorded	GCR							This study

Species	Type of observation	Place of observation	Area	Lat. Grad.	Lat. Min.	Lat. Sec.	Long. Grad.	Lon. Min.	Long. Sec.	Source
Odocoileus virginianus	Hunting	Unrecorded	GCR							This study
Odocoileus virginianus	Hunting	Unrecorded	GCR							This study
Odocoileus virginianus	Sighting	TEF	GCR							This study
Odocoileus virginianus	Sighting	A	GCR							This study
Odocoileus virginianus	Sighting	Unrecorded	GCR							EZM
Odocoileus virginianus	Hunting	Unrecorded	GCR							This study
Odocoileus virginianus	Hunting	Unrecorded	GCR							This study
Odocoileus virginianus	Hunting	Unrecorded	GCR							This study
Odocoileus virginianus	Sighting	Unrecorded	GCR							EZM
Odocoileus virginianus	Sighting	SG	GCR							This study
Odocoileus virginianus	Sighting	TEF	GCR							This study
Odocoileus virginianus	Sighting	SG	GCR							This study
Odocoileus virginianus	Sighting	SG	GCR							This study
Odocoileus virginianus	Sighting	SG	GCR							This study
Odocoileus virginianus	Sighting	Unrecorded	GCR							EZM
Odocoileus virginianus	Sighting	SG	GCR							This study
Odocoileus virginianus	Sighting	TEF	GCR							This study
Odocoileus virginianus	Sighting	SG	GCR							This study
Odocoileus virginianus	Hunting	Unrecorded	GCR							This study
Odocoileus virginianus	Hunting	Unrecorded	GCR							This study
Odocoileus virginianus	Hunting	Unrecorded	GCR							This study
Odocoileus virginianus	Hunting	Unrecorded	GCR							This study
Odocoileus virginianus	Hunting	Unrecorded	GCR							This study
Odocoileus virginianus	Sighting	TEF	GCR							This study
Odocoileus virginianus	Sighting	A	GCR							This study
Odocoileus virginianus	Hunting	Unrecorded	GCR	18	8	10	89	45	28	This study
Odocoileus virginianus	Sighting	Unrecorded	GCR							EZM
Odocoileus virginianus	Sighting	SG	GCR							This study
Odocoileus virginianus	Sighting	A	GCR							This study
Odocoileus virginianus	Sighting	SG	GCR	18	8	10	89	45	28	This study
Odocoileus virginianus	Sighting	A	Nuevo Becal	18	42	30	89	10	30	This study
Odocoileus virginianus	Sighting	TEF	Nuevo Becal	18	47	30.19	89	11	41.68	This study
Odocoileus virginianus	Sighting	TEF	Nuevo Becal	18	37	11.97	89	15	29.1	This study

Species	Type of observation	Place of observation	Area	Lat. Grad.	Lat. Min.	Lat. Sec.	Long. Grad.	Lon. Min.	Long. Sec.	Source
Odocoileus virginianus	Sighting	TEF	Nuevo Becal	18	37	11.97	89	15	29.1	This study
Odocoileus virginianus	Hunting	Unrecorded	GCR	18	36	30.53	89	16	23.17	This study
Odocoileus virginianus	Hunting	Unrecorded	GCR	18	40	0.82	89	15	5.75	This study
Odocoileus virginianus	Hunting	Unrecorded	GCR							This study
Odocoileus virginianus	Hunting	Unrecorded	GCR	18	39	58.06	89	12	43.72	This study
Odocoileus virginianus	Sighting	Temporary transects	Nuevo Becal	18	44	50.21	89	17	56.43	This study
Odocoileus virginianus	Sighting	Temporary transects	Nuevo Becal	18	35	30	89	25	0	This study
Odocoileus virginianus	Sighting	Permanent transects	Nuevo Becal	18	41	21.75	89	12	57.35	This study
Odocoileus virginianus	Sighting	TEF	Nuevo Becal	18	39	58.06	89	12	43.72	This study
Odocoileus virginianus	Hunting	Unrecorded	GCR	18	35	26.94	89	15	30.08	This study
Odocoileus virginianus	Hunting	Unrecorded	GCR	18	36	30.53	89	16	23.17	This study
Odocoileus virginianus	Sighting	TEF	Nuevo Becal	18	34	3.91	89	16	58.8	This study
Odocoileus virginianus	Sighting	A	Nuevo Becal	18	41	21.75	89	12	57.35	This study
Odocoileus virginianus	Sighting	Unrecorded	Nuevo Becal	18	39	58.06	89	12	43.72	This study
Odocoileus virginianus	Sighting	Unrecorded	Nuevo Becal	18	37	10	89	17	49	This study
Odocoileus virginianus	Sighting	Unrecorded	Nuevo Becal	18	35	40.18	89	19	34.73	This study
Odocoileus virginianus	Sighting	Unrecorded	GCR	18	8	10	89	45	28	This study
Odocoileus virginianus	Sighting	TEF	GCR							This study
Odocoileus virginianus	Sighting	A	GCR							This study
Odocoileus virginianus	Sighting	A	GCR							This study
Odocoileus virginianus	Sighting	Unrecorded	GCR							EZM
Odocoileus virginianus	Sighting	Unrecorded	GCR							EZM

Appendix III.

List of plant families and species, parts eaten (Fr: whole fruit; Fl: flower; Se: seed; Le: leaves; St: stem; R: root and Ma: macromicetum fungi) and relative value index of usage (++++ more than 0.1; +++ between 0.01 and 0.1; between 0.001 and 0.01 and T = traces) of plants used as food by the two brocket deer (*Mazama americana* and *Mazama pandora*) and the white-tailed deer (*Odocoileus virginianus*) in the Greater Calakmul Region, Campeche, Mexico from 1996 to 2001.

Family	Species	*M. americana*	*M. pandora*	*O. virginianus*
Acanthaceae	*Bravaisia berlanderiana*			Fr(2), +
Anacardiaceae	*Metopium brownei*	Fr(1), +	Fr(1), +	Fr(3), +
Annonaceae	Unknown	Se(1), T		
Apocynaceae	*Thevetia aohuai*			Fr(1)
	Thevetia gaumeri		Fr(2), ++	Fr(2), ++
Araceae	Unknown			Le(1), T
Araleaceae	*Dendropanax arboreus*	Fr(1), Fl(1), +	Fr(1), +	
Bombacaceae	*Pseudobombax ellipticum*	Fr(3), Fl(1), +		Fl(1)
Boraginaceae	Unknown		Le(1), St(2), +	
Compositae	Unknown			St(1), +
Ebenaceae	Unknown			St(1), T
Erythroxilaceae	Unknown		St(1), +	St(1), +
Euphorbiaceae	Unknown		Le(1), St(2), +	Se(1), +
Flacourtaceae	*Casearia emarginata*			Fr(2), T
	Xylosma flexuosum	Fr(1), +		
Graminae	Unknown		Le(1), +	Le(1), +
Guttifera	*Calophylum brasiliense*		Fr(1), T	
Lauraceae	*Nectandra salicifolia*	Fr(2), ++	Fr(1), Le(3), ++	Le(3), ++
	Unknown			St(1), +
Leguminosae	*Dalbergia glabra*			Le(2), T
	Erythrina standleyana			St(1), T
	Haematoxylum campechianum			Fr(1), ++
	Lysiloma latisiliqua	Fl(1), +		Fl(1), Le(1), +
	Swartzia cubensis		Fr(2), T	
	Swartzia spp.	Le(3), +	Le(4), St(5), +	Le(1), St(3), +
Lorantaceae	Unknown		Le(1), T	
Malpighiaceae	*Byrsonimia crassifolia*		Fr(2), +	Fr(1), +
	Byrsonimia bucidaefolia			Fr(1), +
	Malpighia lundelli		Fr(1), T	
Malvaceae	*Hampea trilobata*	Fr(1), +		Fr(1), Le(2), +
	Malvaviscus arboreus	Fr(1), T		Fr(1), T
Menispermaceae	*Hyperbaena winzerlingii*		Fr(1), +	Fr(2), +
Moraceae	*Brosimum alicastrum*	Fr(7), Le(2), Se(2), ++++	Fr(9), Le(3), ++++	Fr(6), Le(3), ++++
	Castilla elastica		Fr(1), +	
	Pseudolmedia spuria	Se(1), ++	Fr(2), Le(1), +	
	Trophis racemosa	Se(1), +	Fr(1), +	
	Unknown	Fr(2)		Fr(1), St(1), +

continue Appendix III.

Family	Species	*M. americana*	*M. pandora*	*O. virginianus*
Myrcinaceae	Unknown	Fr(1), T		
Myrtaceae	*Eugenia aeruginia*			Fr(1), +
	Eugenia winzerlingii	Fr(1), ++		
	Eugenia spp.	Fr(3), Le(3), ++	Le(6), St(10), ++	Le(6), St(3), ++
	Pimenta dioica	Fr(1), +		
Nycataginaceae	Unknown			Le(1), T
Opiliaceae	*Agonandra macrocarpa*		Fr(1), T	
Orchidaceae	Unknown orchid		Le(1), T	Le(1), St(1), T
Palmae	*Chamaedora ernesti-augusti*	Fr(1), Se(1), +++		
	Chamaedora spp.	Fr(3), ++	Fr(1), +	Fr(1), +
	Cryosophilla argentea	Fr(1), Se(1), ++	Fr(1), +	Se(1), +
	Gaussia maya	Fr(1), +	Fr(1), Se(1), +	Se(1), +
	Sabal mauritiformis	Fr(1), Se(1), ++	Fr(2), ++	
	Sabal mexicana	Fr(1), +		
Piperaceae	Unknown		St(1), T	
Polygonaceae	*Gymnopodium floribundum*		Fr(1), T	Le(1), T
Rhamnaceae	*Krugiodendrum ferreum*		Fr(1), +	
Rubiaceae	*Asemantha pubescens*		Fr(1), T	
	Guettarda gaumeri			Fr(1), +
	Guettarda spp.			Le(1), T
Rutaceae	*Amyris elemifera*			Le(1), +
	Unknown		Se(1), T	Le(1), +
Sapindaceae	*Talisia floresi*		Se(1)	
Sapotaceae	*Manilkara zapota*	Fr(6), ++++	Fr(7), ++++	Fr(3), Se(1), +++
	Pouteria amigdalina	Se(1), +	Fr(1), +	Se(1), +
	Syderoxylum foetidissimum		Fr(2), +	Fr(1), ++
Theophrastaceae	*Jacquinia macrocarpa*		Fr(1), T	
	Unknown		Le(1)	
Unidentified fungi		Ma(2), T	Ma(1), T	Ma(1), T
Unidentified root				R(1), T
Unidentified plant		Le(5), St(5), ++	Fr(1), Fl(1), Se(1), Le(12), St(7), ++++	Se(1), Le(11), St(16), ++++
Total number of identified families 36		12	27 26	28 26
Total number of identified species 46		20		
Total number of UBADPM 32		10	13	11

UBADPM = Unidentified but anatomically different plant material likely belonging to different plant taxa. Nomenclature after Martinez, E. *et al.* (2001). Representative voucher specimens of all seeds were deposited at the National Herbarium (MEXU) National University of Mexico, Mexico City.